

**INFRAESTRUCTURAS ECOLÓGICAS Y CONTROL BIOLÓGICO POR
CONSERVACIÓN EN EL OLIVAR**

**ECOLOGICAL INFRASTRUCTURES AND CONSERVATION BIOLOGICAL
CONTROL IN OLIVE GROVES**

**TESIS DOCTORAL
DANIEL PAREDES LLANES
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CONTROL IN OLIVE GROVES**

Memoria que presenta el Licenciado en Ciencias Ambientales D. Daniel Paredes Llanes
para optar al grado de Doctor.

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VºBº

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Granada, Febrero 2014

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Resumen

La forma convencional de controlar las plagas en agricultura se basa en el uso de productos químicos de síntesis, aunque la mayoría de ellos no parecen ser muy saludables para las personas y ni para los ecosistemas. Por esto, desde muchas y distintas instituciones regionales, nacionales e internacionales se fomenta el objetivo genérico de reducir el uso de estas sustancias y que el manejo de plagas se ejecute por medio de artes y prácticas mucho más sostenibles y respetuosas con la naturaleza.

El control biológico de plagas se lleva a cabo mediante distintas estrategias. Entre ellas se encuentra el “control biológico por conservación”. Existen varias técnicas para llevar a cabo esta estrategia entre las que se encuentra el “manejo de hábitat” cuyo objetivo general es mejorar, proteger y aumentar la diversidad de hábitat para favorecer la abundancia, diversidad y eficacia de los enemigos naturales de las plagas, proporcionándoles recursos básicos (como son alimento en forma de polen y néctar, refugio, presas alternativas...) necesarios para su establecimiento y permanencia en el cultivo. El aumento de la diversidad de hábitat es llevado a cabo mediante la instalación y conservación de infraestructuras ecológicas tanto a nivel de parcela como a nivel de paisaje.

La tipología de paisajes del olivar es muy variada. Teniendo en cuenta que una mayor diversidad de infraestructuras ecológicas (arbolado, cubierta vegetal espontánea, manchas de vegetación natural, muretes de piedra seca, etc.) permite una gran diversidad de hábitats y, por tanto, de beneficios específicos en forma de servicios

ecosistémicos, entre los que se encuentra el control biológico, es plausible llevar a cabo estudios que permitan conocer los efectos que tienen estas infraestructuras ecológicas en el control biológico de plagas. Los resultados obtenidos de estos estudios optimizarían la estrategia de control biológico de plagas por conservación.

Esta tesis doctoral tiene como objetivo último reducir la aplicación de productos químicos de síntesis en olivares mediante la creación de paisajes agrarios funcionales que proporcionen el servicio ecosistémico de control de plagas. Para ello, como primer paso, se intentó determinar el efecto de diferentes infraestructuras ecológicas del agroecosistema del olivar en el control biológico por conservación.

Inicialmente se planteó conocer los posibles efectos conjuntos de las cubiertas vegetales y de la vegetación adyacente al olivar (manchas de vegetación herbácea y grandes y pequeñas manchas de vegetación leñosas) sobre la abundancia de enemigos naturales y de las plagas *Prays oleae* y *Euphyllura olivina*.

Arañas y parasitoides fueron más abundantes en parcelas con cubierta vegetal mientras que esta estructura no afectó a los heterópteros depredadores. Las grandes manchas de vegetación leñosa y herbácea influyeron más en la abundancia de enemigos naturales que las manchas pequeñas. Así pues, el efecto de la vegetación natural adyacente fue diferente para cada grupo y dependió de la presencia de cubierta vegetal.

Cuando ambas estructuras estaban presentes en el cultivo, parasitoides y arañas se vieron influenciados positivamente por la vegetación adyacente, mientras que este efecto fue menor e incluso opuesto en zonas de suelo desnudo, sobre todo en el caso de las arañas con las manchas de vegetación herbácea.

En vista de los efectos que la cubierta vegetal causa en las poblaciones de arañas y parasitoides, cabría esperar que en zonas en las que esta estructura estuviera presente las poblaciones de plagas fuesen menores que en aquellas zonas con suelo desnudo. No obstante, en el estudio se muestra que la cubierta vegetal ejerció un efecto nulo en la abundancia de *P. oleae* y *E. olivina*. Por el contrario, las manchas de vegetación natural sí que tuvieron un efecto positivo en el control biológico de estas plagas. En concreto, la

presencia grandes manchas de vegetación leñosa redujo la abundancia de *P. oleae* y la de pequeñas manchas de vegetación leñosa disminuyó la abundancia de *E. olivina*.

A continuación y debido a las controversias observadas se decidió profundizar en el estudio de las relaciones entre distintos grupos de enemigos naturales y las plagas mencionadas. Se detectó que sólo una especie, *Anthocoris nemoralis*, o un conjunto pequeño de ellas, conformado por *Chrysoperla carnea* y especies pertenecientes a las familias de arañas Araneidae y Liniphiidae, estaban asociadas a menores abundancias de *P.oleae* que conjuntos más complejos de enemigos naturales.

Al parecer, la abundancia de plagas parece estar más sujeta a la presencia de manchas de vegetación natural y de los enemigos naturales que éstas albergan, que a la presencia de cubierta vegetal. No obstante, se detectó que ciertas circunstancias, sobre todo de orden paisajístico y climático, podrían determinar el papel de la cubierta vegetal en el control biológico de plagas.

Ante el riesgo de llegar a conclusiones erróneas o al menos de escasa valía, por no tener en cuenta las características mencionadas se decidió analizar el efecto de la cubierta vegetal ampliando mucho más la escala espacial y temporal de zonificación del estudio. Este análisis aportó evidencias mucho más sólidas acerca de la utilidad de la cubierta vegetal en el control biológico por conservación de plagas del olivo.

Los resultados indicaron que la cubierta vegetal, como una sola entidad y comparada con suelo desnudo, no es una medida efectiva para reducir la abundancia de las plagas *Bactrocera oleae*, *P. oleae*, *Saissetia oleae* y *E. olivina* en olivares. Sin embargo, la variabilidad explicada por factores aleatorios relacionados con las condiciones propias de la parcela (escala local), el contexto paisajístico (escala de paisaje) y de los cambios climáticos entre años (escala regional) fue mucho mayor que la debida a la cubierta vegetal.

Los conocimientos adquiridos en esta tesis doctoral pueden tener aplicaciones prácticas al permitir diseñar estrategias de implementación de manejo de hábitat en olivares en relación con el control biológico de plagas por conservación, ya que se han identificado determinadas infraestructuras ecológicas que parecen adecuadas para ello.

Así, en el caso de *Prays oleae* sería recomendable la presencia de vegetación herbácea y de grandes zonas de vegetación leñosa adyacente al olivar, mientras que en zonas con graves problemas de *Euphyllura olivina* sería aconsejable la presencia de pequeñas zonas de vegetación dentro del cultivo.

Otro interesante aspecto de aplicación sobre los conocimientos adquiridos es el referido a la protección y el incremento de las poblaciones del heteróptero *Anthocoris nemoralis* dada su incidencia sobre la generación antófaga de *P. oleae*.

Aunque a lo largo del estudio y a tenor de los resultados que se exponen no se ha observado un impacto claro de la cubierta vegetal en el control biológico de las cuatro importantes plagas mencionadas; ésta, sin duda, contribuye a aumentar la heterogeneidad de hábitat a nivel local, mostrando su utilidad para mantener poblaciones de artrópodos beneficiosos en el campo de cultivo.

Sería aconsejable, pues, llevar a cabo estudios mucho más detallados; por ejemplo sobre su composición botánica, su distribución espacial, sus artes de manejo... con el objetivo de optimizar su papel en el control biológico por conservación. En cualquier caso, la cubierta vegetal es recomendada para mejorar otros servicios ecosistémicos como son el reciclado de nutrientes, la prevención de la erosión o el aumento de la polinización.

Esta tesis doctoral aporta nuevos conocimientos sobre el efecto de distintas infraestructuras en el control biológico de plagas tanto a nivel general como a nivel específico en el olivar. Las conclusiones reflejadas en este estudio son un primer paso para abordar de forma más óptima la creación de directrices de manejo de infraestructuras ecológicas, de forma que se optimice el uso de métodos alternativos de control y, de esta forma, aumentar la calidad de las cosechas y la salud de las personas.

Summary

The traditional way of controlling pests in agriculture is based on the use of chemical products, most of them harmful to people and the environment. As a result, public and private institutions are lobbying to reduce the application of these substances and turn pest management into more sustainable practices. Pest control can be carried out through several strategies such as conservation biological control. There are several techniques to perform this strategy, one of which is “habitat management”. The aim of this technique is to improve, protect and enhance habitat diversity to favour the abundance, diversity and effectiveness of natural enemies.

In olive groves, landscape types are varied. Taking into account that a greater diversity of ecological infrastructures (trees, ground cover, patches of natural vegetation, walls of stones, etc.) allows a greater habitat diversity and, therefore, specific benefits, it is essential to conduct studies focused on understanding the effects that these infrastructures produce in the biological control of pests. This thesis aims to determine the effect of different ecological infrastructures on the conservation biological control of olive pests. To achieve this, we first investigated the possible combined effects of ground cover and adjacent natural vegetation (herbaceous and large patches of vegetation and small patches of woody vegetation) on the abundance of natural enemies as well as on the pests *Prays oleae* and *Euphyllura olivina*.

Spiders and parasitoids were more abundant in plots with ground cover while this structure did not affect predatory Heteroptera. Large patches of woody and herbaceous

vegetation influenced the abundance of natural enemies more than small patches. The effect of adjacent natural vegetation was different for each group and was dependent on the presence of vegetation cover. When both structures were in the crop, adjacent vegetation had a positive influence on parasitoids and spiders. This effect was less or even opposed in areas of bare soil, especially in the case of herbaceous vegetation patches for spiders.

In view of the effects that ground cover cause on spiders and parasitoids, one would expect pest populations to be consequently reduced. However, it was found that ground cover had no effect on the abundance of *P. oleae* and *E. olivina*. Patches of natural vegetation, on the contrary, had a positive effect on the biological control of these pests. In particular, large areas of woody vegetation reduced the abundance of *P. oleae* and small patches of woody vegetation decreased the abundance of *E. olivina*.

Because of the controversies reported in former studies, it was decided to deepen in the relationships between different groups of natural enemies and the aforementioned pests. It was found that only one species, *Anthocoris nemoralis*, or a small assemblage of them, consisting of *Chrysoperla carnea* and the spider families Araneidae and Liniphiidae, were associated to lower abundances of *P. oleae* than more complex assemblages.

Apparently, the abundance of pest species is more influenced by the presence of patches of natural vegetation and the natural enemies that they can harbour, than by the presence of ground cover within the crop. However, certain circumstances (landscape context or climatic features) that have been identified could determine the role of ground cover in the biological control of these pests. These circumstances could be masking the true effect of ground cover; drawing useless conclusions if studies do not consider these features and are conducted at local scales. To address this issue, the effect of ground cover was analysed in several hundreds of orchards located across a large study region (Andalusia) over a seven years period. This study provided sound evidences about the usefulness of ground cover in conservation biological control of olive pests.

The results of this analysis indicated that ground cover, as a single entity and compared with bare soil, is not an effective measure to reduce the abundance of the pest species

Bactrocera oleae, *P. oleae*, *Saissetia Oleae* and *E. olivina* in olive groves. The variability explained by random factors related to the specific conditions of the plot (local scale), the landscape context (landscape scale), and climatic variability amongst years (regional scale) was much higher than that explained by ground cover.

The knowledge gained in this thesis will allow us to design strategies for implementing habitat management in olive orchards since the most suitable ecological infrastructures have been identified in relation to the conservation biological control of pests. For *Prays oleae*, the presence of herbaceous vegetation and large areas of woody vegetation adjacent to the olive grove would be recommendable. In areas with serious problems of *Euphyllura olivina* the presence of small areas of vegetation within the crop would be advisable. Another aspect of interest is to recommend the protection and the increase of populations of the predatory Heteroptera *Anthocoris nemoralis* given its impact on the anthophagous generation of *P. oleae*. Although a clear effect of ground cover on the biological control of four major olive pests was not observed, it contributes to increase habitat heterogeneity at the local level, showing its utility to maintain populations of beneficial arthropods in the field. To optimize the role of ground cover in conservation biological control it would be advisable to conduct further detailed studies on how ground cover species composition, its arrangement in the orchard and its management might affect pests abundance. Anyway, ground cover is recommended to enhance other ecosystem services such as nutrient recycling, prevention of erosion or pollination.

The results of this study aim to provide practical guidelines for the implementation of strategies for conservation biological control in olive groves. This seems a promising option since one of the objectives of conservation biological control is to develop the strength of natural resources in relation to the biological control of pests. The implementation of this strategy will reduce the use of pesticides, while ensuring the production of higher quality products, the protection of the environment and the sustainability of this important crop.



1

Introducción

Este capítulo reproduce parcialmente los siguiente artículos:

Paredes D, Campos M, Cayuela L. 2013. El control biológico de plagas de artrópodos por conservación: técnicas y estado del arte. *Ecosistemas* 22(1): 56-61.

Paredes D, Mercedes M. 2013. Importancia de la biodiversidad en la gestión integrada de plagas en el cultivo del olivar. *Vida Rural* 363: 30-34.

La facilidad que proporciona el uso de productos químicos de síntesis para controlar plagas ha derivado en la consolidación de métodos de cultivo basados en el uso generalizado de pesticidas. Junto con esta práctica han aparecido una serie de problemas que amenazan tanto la sostenibilidad y la calidad de las cosechas como la salud de las personas y de los sistemas naturales (Meehan et al. 2011). Para frenar esta tendencia, sectores del ámbito social, científico y político reclaman a los profesionales del agro un cambio en el manejo de plagas dirigido hacia estrategias más sostenibles. En esta línea, el nuevo Real Decreto de 2012 sobre el uso sostenible de fitosanitarios enfatiza “*la promoción de los mecanismos naturales de control de plagas*”. Para ello se ha de adoptar un Plan de Acción Nacional que debe, entre otras cosas, “*contribuir a garantizar la biodiversidad mediante la conservación de los hábitats naturales y de la fauna y flora silvestres*”, algo novedoso que muestra una nueva orientación en la aplicación del control biológico en la gestión integrada de plagas.

1.1 El control biológico

El **control biológico** es definido como: “*el uso de organismos para suprimir la densidad de población o el impacto de un organismo plaga específico, haciéndolo menos abundante de lo que sería si no se usaran dichos organismos*” (DeBach 1964). El término organismos vivos es bastante amplio e incluiría desde microorganismos hasta animales superiores. En control biológico se utilizan los vocablos enemigos naturales, fauna auxiliar u organismos beneficiosos para denominar a aquellos agentes del agroecosistema que pueden actuar contra las plagas. En el caso de plagas de artrópodos controladas por otros artrópodos, el control es llevado a cabo mediante dos procesos fundamentales: la depredación y el parasitismo. Dentro del grupo de depredadores potenciales de plagas se encuentran los órdenes Coleóptera, Odonata,

Neuroptera, Hymenoptera, Araneae, Diptera y Hemiptera (**Figura 1a-f**). Los artrópodos depredadores se alimentan de todos los estados de la presa: huevos, larvas (o ninfas), pupas y adultos. Los principales grupos de parasitoides utilizados en el control biológico de plagas pertenecen a los órdenes Hymenoptera (la mayoría son avispas de las superfamilias Chalcidoidea, Ichneumonoidea y Proctotrupeoidea) y Diptera (moscas, especialmente de la familia Tachinidae).

Eliengber et al. (2001), en un artículo que trata de unificar el término control biológico, determinan cuatro estrategias complementarias: (1) el **control biológico clásico**, que define como *“la introducción intencionada de un agente de control biológico exótico, normalmente coevolucionado con la plaga, para establecerlo permanentemente y controlar la plaga a largo plazo”*; (2) el **control biológico por inoculación**, cuya definición se apoya en aquella propuesta por Crump (1999), y se refiere a *“la suelta intencionada de un organismo vivo como agente de control biológico con el objetivo de que se multiplicará y controlará la plaga durante un periodo, pero no permanentemente”*; (3) el **control biológico por inundación**, cuya definición se inspira en aquella de van Driesche y Bellows (1996), haciendo referencia a *“el uso de organismos vivos para controlar plagas cuando el control es logrado exclusivamente por los organismos liberados”*; y (4) el **control biológico por conservación**, el cual *“se basa en la modificación del medio ambiente o de las prácticas existentes para proteger y aumentar los enemigos naturales específicos u otros organismos con la finalidad de reducir el efecto de las plagas”* (DeBach 1964).

Principalmente, el control biológico por conservación (CBC) se diferencia de las otras estrategias de control biológico en que no se realizan sueltas de individuos, sino que pretende establecer, mediante la aplicación de determinados métodos, un entorno ambiental adecuado en el que se desarrolle el cultivo (Barbosa 1998). En el caso de los artrópodos, la aplicación de estos métodos no ejerce por sí misma la acción de controlar las plagas, sino que promueve la abundancia, diversidad y eficacia de los enemigos naturales ya presentes en el agroecosistema.

Así, la conservación de enemigos naturales es, probablemente, la forma más antigua de control biológico de plagas. Ya en el año 900 DC, citricultores chinos emplazaban nidos de la hormiga tejedora *Oecophylla smaragdina* F. en campos de cultivo de

naranjos para reducir las poblaciones de insectos que se alimentaban de las hojas (Sweetman 1958).

No obstante, no se empezó a tener conciencia de este nuevo campo de la ciencia hasta que, en una de las primeras revisiones sobre esta materia, Sweetman (1958) describió algunos métodos que venían siendo utilizados desde hacía algunos años. Estos pasaban por conservar los enemigos



Figura 1.1 Enemigos naturales, plagas y manejo de hábitat. a: *Prays oleae*, plaga del olivo b: *Chrysoperla carnea* depredando una larva de *P. oleae*; c: *Aranelia curcubitina*; d: Ninfa de *Deraeocoris punctum*, heteróptero depredador; e: *Chsytolina bankii*; f: *Anthocoris nemoralis*, depredador en cultivos perennes; g: Cubierta vegetal en olivar.

naturales plantando cultivos insectarios. Más tarde van den Bosch y Telford (1964) publicaron una revisión bibliográfica más exhaustiva que tuvo en cuenta la modificación del medio ambiente para llevar a cabo un control biológico de las plagas. Algunas de las técnicas sugeridas por estos autores para promover el control biológico por conservación incluían la construcción de estructuras artificiales (capaces de dar refugio y lugares de anidamiento a los enemigos naturales), la provisión de alimento suplementario como néctar o polen, el

suministro de huéspedes alternativos, la mejora de la sincronía plaga-enemigo natural, el control de las hormigas y la modificación de prácticas agronómicas adversas. La siguiente gran revisión es la realizada por Rabb et al. (1976), en donde se reconoce que la mayoría de las técnicas son potencialmente útiles, si bien tienen poco valor para el control de plagas.

Sin embargo, la llegada de Miguel Ángel Altieri al panorama científico da una vuelta de tuerca al paradigma del control biológico por conservación. Altieri y sus colaboradores

enfocan el problema desde una nueva óptica: la perspectiva agroecológica. Este nuevo enfoque surge como respuesta al cambio que están sufriendo las prácticas agrícolas en occidente, con una tendencia clara hacia el monocultivo, un incremento de la superficie del mismo y una pérdida de la diversidad local del hábitat, hecho que repercute de manera directa en la abundancia, diversidad y eficacia de los enemigos naturales (Altieri y Letourneau 1982). Un aumento en la diversidad vegetal en el agroecosistema derivaría en un incremento de las oportunidades ambientales de los enemigos naturales y, consecuentemente, en la mejora del control biológico (Altieri y Nicholls 2007). Los sistemas agrícolas tradicionales han utilizado la biodiversidad para protegerse de plagas y enfermedades, minimizando el riesgo de pérdida del cultivo, produciendo una dieta variada y diversificando las fuentes de ingresos económicos (Altieri 1991a). Por el contrario, los sistemas modernos de agricultura se han caracterizado por la especialización, a expensas de la diversidad, lo cual ha derivado en una menor resistencia al ataque de las plagas (Altieri y Letourneau 1982).

En el contexto agroecológico se establece la idea de que el control biológico por conservación no necesita de la realización de acciones puntuales sino que se trata, más bien, de crear un entorno que establezca las relaciones entre cultivo, plaga y enemigos naturales, evitando fluctuaciones en las poblaciones que hagan perder la producción. Esta estabilidad sería consecuencia directa de la biodiversidad contenida en el agroecosistema (Altieri y Letourneau 1982; Gliessman 2007), la cual se vería incrementada mediante diversas técnicas. Los métodos utilizados han ido evolucionando desde las primeras prácticas sugeridas por van den Bosch y Telford en 1964 hasta la actualidad y pueden agruparse en dos aproximaciones fundamentales: el manejo de hábitat y la ecología química. No obstante, las prácticas más novedosas que se están llevando a cabo en el ámbito del control biológico por conservación combinan ambas técnicas.

1.2 El manejo del hábitat

La mayoría de las técnicas encaminadas a la optimización del control biológico por conservación se pueden englobar bajo el término manejo de hábitat. En una de las obras que más impacto ha tenido en el ámbito del control biológico, Landis et al. (2000) establecen los principios del manejo de hábitat para la conservación de enemigos naturales de plagas de artrópodos en agricultura. Estos autores definen el manejo del

hábitat como un método del control biológico por conservación que se basa en la modificación del hábitat para mejorar la disponibilidad de los recursos requeridos por los enemigos naturales para que su acción contra las plagas sea óptima. Esta mejora es realizada mediante la instalación o el manejo de las infraestructuras ecológicas adecuadas, tanto en el campo de cultivo como en el paisaje en el que se encuentra inmerso, para proporcionar a los enemigos naturales alimento, presas o huéspedes alternativos, y refugio cuando las condiciones del cultivo sean adversas. Estas infraestructuras ecológicas se encuentran tanto dentro como fuera de la finca y pueden ser setos, manchas de vegetación leñosa o herbácea, cubiertas vegetales o incluso muros de piedra (Boller et al. 2004).

Hasta la fecha han sido numerosos los trabajos que han estudiado la influencia del manejo del hábitat sobre la abundancia y diversidad de enemigos naturales. Además, son múltiples las técnicas que se pueden llevar a cabo, las cuales están sujetas a las características del cultivo donde se apliquen. Se podría hacer una división entre cultivos anuales y perennes ya que las diferencias de manejo entre ambos exigen la aplicación de aproximaciones distintas.

En cultivos anuales, se producen grandes perturbaciones periódicas que perjudican el establecimiento de poblaciones de enemigos naturales (Altieri 1991b). La reducción de dichas poblaciones deteriora el potencial de control biológico y necesita de la colonización del nuevo cultivo recién plantado desde fuentes naturales, la cual tiene muchas posibilidades de ser débil y tardía (Perdikis et al. 2011). Por ello, es muy importante promover infraestructuras ecológicas que sean capaces de atraer a estos artrópodos beneficiosos hacia el campo de cultivo y que maximicen sus posibilidades de supervivencia cuando se produce una perturbación, de forma que posteriormente puedan colonizar de nuevo el cultivo (Thomas et al. 1992).

Para conseguir atraer a insectos beneficiosos hacia los campos de cultivo anuales la técnica más utilizada es la siembra de franjas de herbáceas florales. Este método ha dado buenos resultados con especies como *Fagopyrum esculentum*, la cual atrae parasitoides y coccinélidos hacia campos de repollo y soja respectivamente (Lee y Heimpel 2005; Woltz et al. 2012), *Phacelia tanacetifolia*, que incrementa la presencia

de sírfidos en campos de trigo (Hickman y Wratten 1996), o *Panicum maximum*, que aumenta la abundancia de depredadores en campos de maíz (Koji et al. 2007).

Los cultivos perennes son potencialmente más adecuados para llevar a cabo un control biológico por conservación, debido a que están sujetos a menor grado de perturbación que los anuales. En ellos la aproximación más frecuentemente utilizada ha sido la instalación y el manejo de una cubierta vegetal entre las calles del cultivo (**Figura 1g**).

Ésta, normalmente, puede ser en forma de franja entre las líneas de árboles o, menos comúnmente, como un continuo en el suelo (Smith et al. 1996). Esta cubierta vegetal está compuesta típicamente por especies plantadas pertenecientes a las familias Poaceae y Fabaceae, aunque existen estudios en los que se deja crecer la cubierta natural de forma espontánea (Rieux et al. 1999; Silva et al. 2010; Paredes et al. 2013a) y otros en donde el diseño de cubiertas se realiza con plantas aromáticas (Song et al. 2010).

La presencia de cubiertas vegetales ha dado resultados controvertidos en este tipo de cultivos, yendo desde trabajos donde se detectaba efectos muy positivos en la abundancia y la diversidad de enemigos naturales en cultivos de pera (Rieux et al. 1999; Song et al. 2010), nuez pacana (Smith et al. 1996), viñas (Danne et al. 2010), cítricos (Silva et al. 2010) y olivar (Paredes et al. 2013a), a otros trabajos en viñas (Costello y Daane 1998) y manzana (Bone et al. 2009) que no han detectado ningún efecto. De la misma forma, la influencia de las cubiertas vegetales en la abundancia de plagas genera controversias (Simon et al. 2010). Por ejemplo, el uso de cubierta vegetal en melocotoneros puede reducir la abundancia de plagas (Dong et al. 2005; Wan et al. 2011) al igual que puede aumentarla (McClure et al. 1982; Meagher y Meyer 1990a). Asimismo, la presencia de esta infraestructura ecológica en otros cultivos perennes (manzano, pera, cítricos, olivo) no siempre consigue reducir la abundancia de las especies plaga (**Tabla 1.1**).

Otra forma de favorecer las poblaciones de enemigos naturales, especialmente útil en cultivos herbáceos, es el uso de infraestructuras perennes alrededor del cultivo. Cómo esta vegetación es de crecimiento lento, lo habitual no es sembrarla, sino hacer uso de la diversidad paisajística que existe de forma natural en torno al campo de cultivo, en todo caso favoreciéndola.

Tabla 1.1 Revisión de trabajos en los que se analiza el efecto de la cubierta vegetal sobre las plagas. Inspirada y ampliada de Simon et al. (2010).

Cultivo	Plaga	Tratamientos de cubierta vegetal	Efecto en la plaga	Referencia/Región
Cítricos	<i>Frankenella occidentalis</i> y <i>Thrips tabaci</i>	Salvaje, <i>Festuca arundenacea</i> y suelo desnudo	Positivo <i>Festuca arundenacea</i> , Negativo salvaje y suelo desnudo	Aguilar-Fenollosa y Jacas 2013/España
Cítricos	<i>Tetranychus urticae</i>	Salvaje, <i>Festuca arundenacea</i> y suelo desnudo	Positivo <i>Festuca arundenacea</i>	Aguilar-Fenollosa et al. 2011/España
Cítricos	Hemíptera	Salvaje	Nulo	Stevens et al. 2007/Australia
Olivo	<i>Prays oleae</i> y <i>Euphyllura olivina</i>	Salvaje y suelo desnudo	Nulo	Paredes et al. 2013b/España
Olivo	<i>Prays oleae</i> y <i>Bactrocera oleae</i>	Cereal	Variable	Rodríguez et al. 2009/España
Melocotón	<i>Lyonetia clerkella</i>	<i>Medicago sativa</i> y salvaje	Positivo <i>Medicago</i>	Dong et al. 2005/China
Melocotón	<i>Aromia bungii</i> y <i>Halyomorpha halys</i>	<i>Trifolium repens</i> y suelo desnudo	Negativo	Wan et al. 2011/China
Melocotón	<i>Tetranychus urticae</i>	Salvaje, suelo desnudo, <i>Vicia angustifolia</i>	Negativo con <i>Vicia angustifolia</i>	Meagher y Meyer 1990a/EE.UU.
Melocotón	Saltadores de hoja vectores de enfermedades	<i>Trifolium pretense</i> , mezcla de especies rosáceas, <i>Dactylis glomerata</i> y suelo desnudo	Negativo	McClure et al. 1982/EE.UU.
Melocotón	Hemípteros	Suelo desnudo, césped en bandas y césped continuo	Negativo	Meagher y Meyer 1990b/EE.UU.
Manzano	Manzano plagas	Salvaje	Positivo	Altieri y Smith 1985/EE.UU.
Manzano	Spider mites	Salvaje	Nulo	Nyrop et al. 1994/EE.UU.
Manzano	<i>Dysaphis plantagenea</i> y <i>Aphis pomi</i>	Franjas de hierba y suelo desnudo	Positivo	Wiss 1995/Suiza
Manzano	Leafroller	<i>Fagopyrum esculentum</i>	Positivo	Stephens et al., 1998/Nueva Zelanda
Manzano	Manzano plagas	Salvaje	Nulo	Jenser et al., 1999/EE.UU.
Manzano	Aphis spp.	Plantada, salvaje, hierba segada y suelo desnudo	Nulo	Marko et al., 2013/Hungría
Manzano	<i>Helicoverpa armigera</i>	Mezcla de varias semillas	Nulo	Bone et al. 2009/Australia
Manzano	Aphis spp.	<i>Phacelia tanacetifolia</i> , <i>Fagopyrum esculentum</i> y una mezcla de especies de Poaceas	Nulo	Frechette et al. 2008/Canadá
Viñas	<i>Erythroneura elegantula</i> y <i>Frankliniella occidentalis</i>	<i>Fagopyrum esculentum</i>	Positivo	Nicholls et al. 2000/EE.UU.
Viñas	<i>Erythroneura</i> spp.	Salvaje y suelo desnudo	Nulo	Costello y Danne 2003/EE.UU.
Viñas	<i>Erythroneura</i> spp.	<i>Fagopyrum esculentum</i> , <i>Trifolium repens</i> y <i>Dactylis glomerata</i>	Nulo	English-Loeb et al. 2003/EE.UU.
Viñas	Tortricidae	<i>Fagopyrum esculentum</i>	Nulo	Berndt et al. 2006/Nueva Zelanda
Peral	<i>Panonychus ulmi</i> (en Manzano), <i>Cacopsylla pyricola</i> (en Peral)	Mezcla de plantas con flores	Nulo	Fitzgerald y Solomon 2004/Reino Unido
Peral	<i>Cacopsylla pyri</i>	Plantada, salvaje y suelo desnudo	Positivo	Rieux et al. 1999/Francia
Peral	<i>Psylla chenensis</i> , <i>Aphis citricola</i> y <i>Pseudococcus comstocki</i>	Aromáticas, salvaje y suelo desnudo	Positivo	Beizhou et al. 2011/China

El efecto de la cubierta en el control de plagas es considerado positivo, nulo o negativo cuando la densidad de la plaga o el daño que ejerce es menor, igual o mayor, respectivamente, comparado con el control.

Algunos ejemplos son los árboles y arbustos que se encuentran en caminos o lindes entre cultivos, la vegetación riparia o los arbustos localizados en las zonas no cultivables. Si el campo de cultivo está inmerso en un paisaje muy diverso (heterogéneo) las posibilidades de que se ejerza un control biológico por conservación

serán mayores de las que existirían si la actividad agrícola se realizase en un contexto paisajístico poco diverso (homogéneo). Thies y Tschardt (1999) aportaron una de las primeras evidencias de este hecho y llegaron a determinar que el daño que realizaban las plagas al cultivo así como el porcentaje de parasitismo sobre una plaga de colza estaba relacionado, negativa y positivamente respectivamente, con la diversidad del paisaje circundante. Otros estudios han corroborado dicha relación (Bianchi et al. 2006; Chaplin-Kramen et al. 2011).

El hecho de que el contexto paisajístico influya en la calidad del control biológico por conservación ha sido normalmente obviado en estudios que implementaban algunas de las técnicas citadas anteriormente y puede ser la causa de la controversia detectada en el efecto de las cubiertas vegetales. La mayoría de los trabajos se han centrado en la vegetación que no corresponde al cultivo (enfoque de paisaje) o en aquellos derivados de la instalación y mantenimiento de infraestructuras en los campos de cultivo (enfoque de cultivo) (Woltz et al. 2012). Muchos de los estudios que han evaluado las diferentes técnicas de control biológico por conservación no han tenido en cuenta el contexto paisajístico, ignorando así los posibles efectos sinérgicos (tanto positivos como negativos) entre los hábitats seminaturales y las técnicas implementadas (Altieri et al. 2005). No obstante, recientes trabajos en la materia ya contemplan esta posibilidad tanto en cultivo anuales (Woltz et al. 2012) como en cultivos perennes (Paredes et al. 2013a).

1.3 Ecología química

El control biológico por conservación se puede apoyar en otra serie de técnicas como son aquellas derivadas de la aplicación de sustancias sintéticas procedentes del estudio de la ecología química, que trata de entender el lenguaje que utilizan las plantas y los artrópodos para comunicarse y modificar su comportamiento en nuestro beneficio.

Las plantas pueden emitir compuestos volátiles capaces de atraer y repeler a determinados artrópodos. Éstos incluyen sustancias volátiles cuya emisión es inducida por el ataque de un herbívoro a la planta (en adelante HIPVs por sus siglas en inglés) y, en algunos casos, volátiles emitidos por plantas no atacadas. Khan et al. (2008) revisaron cómo estos compuestos pueden ser utilizados en el control biológico por conservación tanto para incrementar el número de enemigos naturales atraídos hacia el campo de cultivo como para repelerlos del mismo. En su trabajo, y basándose en James

(2005), establecen una relación entre los diferentes HIPVs capaces de atraer a distintos enemigos naturales, y por tanto la posibilidad de mejorar el control biológico (**Tabla 1.2**). Estos compuestos son: cis-3-hexen-1-ol, (E)-2-hexen-1-al, cis-3-acetato de hexenilo, salicilato de metilo, indol, antranilato de metilo, cis-jasmonato, geraniol, nonanal, octylaldehído, benzaldehído y farnaseno. Como sustancias repelentes de insectos se encuentran el (E)-ocimene, el α -terpinoleno, el α -cedreno y el b-cariophileno, entre otros. Estas sustancias han sido implementadas únicamente en la técnica de reclutamiento y retirada, la cual se detalla a continuación.

1.4 Combinación manejo de hábitat y ecología química

Estas combinaciones están orientadas a establecer sinergias capaces de cumplir con mayor eficacia los objetivos que plantea el control biológico por conservación. Hasta la fecha se han ideado dos tipos de estrategias: la atracción y recompensa (attract and reward) y el reclutamiento y retirada (push-pull).

1.4.1 Atracción y recompensa

Esta nueva aproximación de control biológico por conservación utiliza dos técnicas: (1) la forma sintética de compuestos volátiles de plantas inducidos por herbívoros para atraer a artrópodos beneficiosos hacia el campo de cultivo (ecología química), y (2) la instalación de plantas con néctar para mantener las poblaciones de estos artrópodos en el mismo (manejo de hábitat).

Simpson et al. (2011) fueron los primeros, y probablemente los únicos, que han investigado acerca de esta combinación de métodos. Sus resultados fueron prometedores y sugieren que la aplicación de HIPVs sintéticos puede aumentar la atracción de enemigos naturales y que las plantas con néctar son un recurso adecuado para incrementar la abundancia y la permanencia de estos artrópodos en el campo de cultivo.

1.4.2 Reclutamiento y retirada

Esta técnica se basa en la manipulación de insectos plaga y sus enemigos naturales a través de la integración de estímulos que convierten el recurso protegido poco atractivo para las plagas, mientras que las desplaza hacia un recurso atractivo distinto del cultivo (Miller y Cowles 1990). Estos estímulos son HIPVs introducidos en el agroecosistema

mediante la instalación de plantas capaces de emitirlos o bien en su forma sintética. Las plagas son repelidas del cultivo principal y son, simultáneamente, atraídas hacia el cultivo trampa. De la misma forma, se pueden utilizar HIPVs para atraer enemigos naturales. Los estímulos repelentes se situarían entre las calles del cultivo mientras que los atrayentes en los bordes del mismo. De esta forma se interfiere en el comportamiento de los artrópodos para modificar la distribución y abundancia de las plagas y de sus enemigos naturales. La mayoría de las experiencias de este tipo han sido llevadas a cabo en África con cultivo de maíz, donde se han detectado que especies vegetales herbáceas como *Pennisetum purpureum* y *Sorghum vulgare* actúan como cultivos trampa mientras que *Melinis minutifolia* y *Desmonium uncinatum* son buenas para repeler a las plagas del maíz (Khan et al. 2001).

Tabla 1.2 HIPVs capaces de atraer a diferentes enemigos naturales (Khan et al. 2008).

Especie, género, familia o grupo	HIPVs												
	A	B	C	D	E	F	G	H	I	J	K	L	M
<i>Chrysopa nigricornis</i>				x									
<i>Stethorus p. picipes</i>	x		x	x									x
<i>Orius tristicolor</i>	x		x	x								x	x
<i>Geocoris pallens</i>		x		x	x								
<i>Deraeocoris brevis</i>			x	x									
<i>Anagrus daanei</i>	x											x	x
<i>Thaumatomyia glabra</i>							x						
<i>Hemerobius</i> sp.				x									
Syrphidae	x			x									
Braconidae	x		x	x		x	x	x					
Empididae				x									
Sarcophagidae				x			x			x	x		x
Agromyzidae				x									
Micro-Hymenoptera	x			x	x								

HIPVs producidos por plantas: A: cis-3-hexen-1-ol; B: (E)-2-hexen-1-al; C: cis-3-acetato de hexenilo; D: salicilato de metilo; E: indol; F: antranilato de metilo; G: cis-jasmonato; H: genranio; I: nonanal; J: octylaldehído; K: benzaldehído; L: farnaseno.

1.5 Diversidad funcional

En teoría, el incremento de la diversidad de enemigos naturales puede aumentar las posibilidades de que alguna de esas especies actúe de manera efectiva contra las plagas (Straub et al. 2008). No obstante, se ha detectado que en la mayoría de los casos la relación entre biodiversidad y control biológico no es exitosa (Moonen y Bàrberi 2008; Sans 2007) y que en aquellos en los que el control biológico es efectivo, es un solo

agente el que ejerce ese control (Denoth 2002). Diferentes procesos ecosistémicos podrían estar detrás del hecho de que no en todas las ocasiones un incremento en la biodiversidad del agroecosistema suponga una supresión efectiva de las poblaciones de los insectos plaga.

Un factor clave que puede desvirtuar la relación positiva entre la biodiversidad y la supresión de una plaga es la depredación intragremial, que ocurre cuando un depredador consume a otro depredador que compite por la misma presa (Polis et al. 1989; Finke y Denno 2004). Este hecho desvía la acción del primero de la especie objetivo (plaga), y disminuye la acción del segundo sobre la plaga por el descenso de su abundancia. Así, un incremento de la biodiversidad en el agroecosistema aumentaría las posibilidades de que este proceso ocurriese, disminuyendo las posibilidades de que se produzca un control biológico.

No obstante, un aumento de la biodiversidad también puede aumentar la redundancia funcional, es decir, el hecho de que varios enemigos naturales realicen la misma función en el agroecosistema (Walker 1992), aumentando así su resiliencia (Martín-López et al. 2007). De esta forma aumenta la posibilidad de control biológico, ya que la disminución de una especie no compromete la función de su grupo. No obstante, los trabajos revisados por Straub et al. (2008) no avalan esta hipótesis ya que incrementos en el número de enemigos naturales de las plagas no conllevan una disminución en la abundancia de plagas.

También es posible pensar que un aumento de la diversidad puede aumentar el rango de estrategias funcionales de consumo de un recurso (plaga) por parte de los diferentes consumidores del mismo, es decir sus enemigos naturales. Así, mientras que un enemigo natural puede perseguir a su presa hasta cazarla, otro puede emboscarse hasta que la presa pase y, de esta forma, cazarla, produciéndose un proceso de complementariedad de nicho que nos lleva hacia una relación positiva entre biodiversidad y control biológico ya que el mismo recurso podría ser explotado por diferentes enemigos naturales.

La ocurrencia de estos sucesos no puede ser estimada partiendo del cálculo de la biodiversidad, por lo que se está cambiando la tendencia hacia el cálculo de la

diversidad funcional. Ésta es uno de los componentes de la biodiversidad descritos por Hooper et al. (2005) la cual se podría definir como *“la diversidad de funciones de los elementos de un ecosistema entendiendo estos como los servicios que proporciona”* (Moonen y Bàrberi 2008). Uno de estos servicios ecosistémicos es el control de plagas. En nuestro contexto se podría definir la diversidad funcional como *“aquella que tiene en cuenta los rasgos biológicos de la fauna auxiliar para identificar la composición óptima de la comunidad que permita controlar las poblaciones de los artrópodos plaga de manera efectiva”*. La definición de estos rasgos es el principal problema a la hora de definir la diversidad funcional de una comunidad. Straub et al. (2008) distingue cuatro rasgos relevantes que deberían ser tenidos en cuenta a la hora establecer la diversidad funcional de una comunidad. Estos son: la preferencia de presa, la respuesta a la densidad de la presa, el uso del microhábitat que hacen los enemigos naturales y la fenología de los mismos. Por lo tanto se cree que la diversidad funcional podría utilizarse como variable predictora del éxito del control biológico por conservación en un agroecosistema determinado. De esta manera se podría evaluar si los procesos anteriormente mencionados se producen dentro del agroecosistema, ampliando el conocimiento sobre las relaciones que se llevan a cabo en él y, en última instancia, pudiendo determinar las técnicas más adecuadas para que el control biológico por conservación actúe de manera efectiva sobre las plagas de los cultivos.

1.6 El cultivo del olivar y control biológico por conservación

El olivar es un cultivo de especial importancia en la región mediterránea ya que ocupa 7,6 millones de hectáreas, de las cuales 2,5 millones se encuentran en España (MAGRAMA 2012), y ofrece unas características óptimas para la implantación de una estrategia de control biológico por conservación basada en el manejo del hábitat. Al ser un cultivo perenne, es fácil la instalación y manejo de una cubierta vegetal en las calles del cultivo.

Además, el olivar se caracteriza por poseer una abundante y diversa comunidad de enemigos naturales con un complejo parasitario representado por unas 300 a 400 especies del orden himenóptera (Arambourg 1986) y un complejo depredador compuesto por distintos órdenes. Entre los principales grupos de depredadores se encuentran las arañas, que es el más diverso con 217 especies, seguido por el orden coleóptera con 30 especies, el grupo de las hormigas con 24, hemípteros con 11 y

neurópteros con 13 (Morris et al. 1999; Redolfi et al. 1999; Ruiz-Torres y Montiel-Bueno 2000; Santos et al. 2007; Cárdenas 2008; Cotes et al. 2010; Rei et al. 2010). No obstante, varios insectos atacan y dañan los olivos, siendo las especies plaga clave la mosca del olivo *Bactrocera oleae* Gmel. (Diptera: Tephritidae) (**Figura 1.2a**), la polilla del olivo *Prays oleae* Bern. (Lepidoptera: Plutellidae) (**Figura 1.2b**), y la cochinilla del olivo *Saissetia oleae* Olivier (Homoptera: Coccidae) (**Figura 1.2c**). Estos tres fitófagos están ampliamente distribuidos y normalmente causan elevados daños en el cultivo reduciendo la cantidad y calidad de la producción (Arambourg 1986; Tzanakakis 2006). Además, existen otras plagas secundarias que de forma más esporádica pueden provocar pérdidas tan importantes como las primeras, y entre ellas se encuentran especies como *Euphyllura olivina* Costa (Hemiptera: Psyllidae) (**Figura 1.2d**), *Phloeotribus scarabaeoides* Bern. (Coleoptera: Scolytidae) (**Figura 1.2e**) o *Euzophera pinguis* Haw. (Lepidoptera: Pyralidae) (**Figura 1.2f**) (Civantos 1999; Alvarado et al. 2008; Campos 2011).

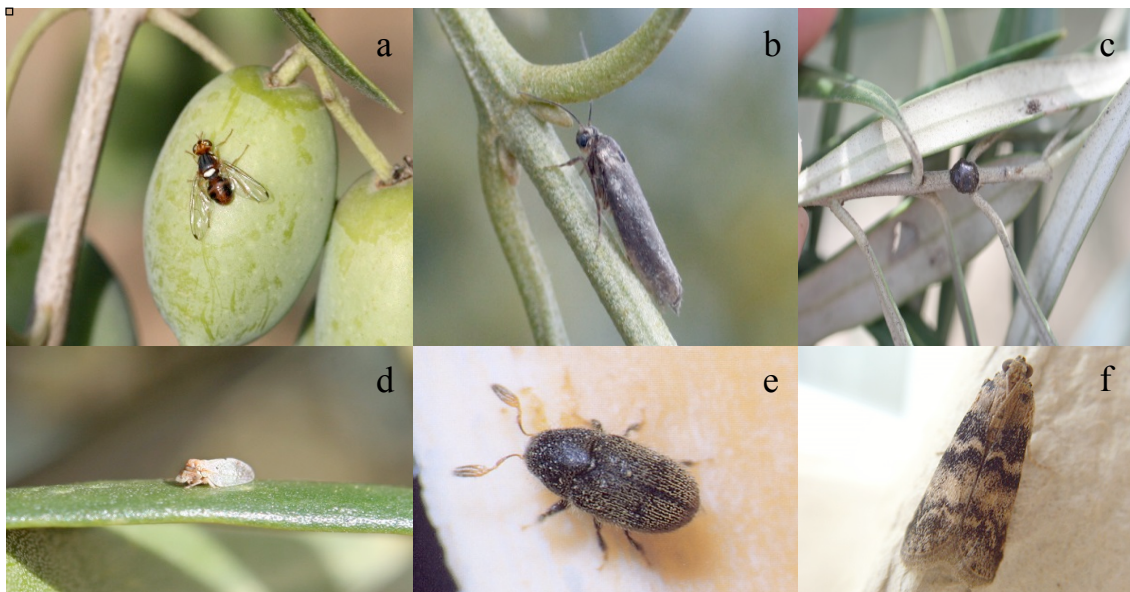


Figura 1.2 Diferentes plagas del olivo. a: *Bactrocera oleae*; b: *Prays oleae*; c: *Saissetia oleae*; d: *Euphyllura olivina*; e: *Phloeotribus scarabaeoides*; f: *Euzophera pinguis*.

El olivar presenta una tipología de paisajes muy variada (Duarte et al. 2009). Si tenemos en cuenta que una mayor diversidad estructural (arbolado, cubierta vegetal espontánea, manchas de vegetación natural, etc.) permite una gran diversidad de hábitat y beneficios específicos, es razonable pensar que cada tipo de olivar deberá plantear su modo particular de relación con la biodiversidad de forma que sea posible compatibilizar su

conservación con el resultado económico. No obstante, los beneficios de la complejidad paisajística han sido escasamente cuantificados en el olivar por lo que es necesario realizar estudios específicos y determinar el peso de cada una de estas infraestructuras ecológicas en relación con el control biológico por conservación, lo que permitirá desarrollar medidas dirigidas a valorizar la acción de la fauna auxiliar y por tanto la sostenibilidad del olivar (Duarte et al. 2009).

1.7 Estructura de la tesis doctoral

El objetivo de esta tesis doctoral es evaluar el potencial de una estrategia de control biológico por conservación en olivares. Para ello se analizó el efecto que determinadas infraestructuras ecológicas (cubierta vegetal y manchas de vegetación natural) tienen en los enemigos naturales y en plagas, como *Prays oleae* y *Euphyllura olivina* (**Figura 2b y d**) (Capítulos 4 y 5). De la misma forma, y debido a controversias en los resultados obtenidos, ya que un aumento en la abundancia de enemigos naturales no repercutió en una reducción de la abundancia de plagas, se profundizó en las relaciones existentes entre los enemigos naturales y las plagas, así como entre los propios enemigos naturales (Capítulo 6). Para corroborar las tendencias observadas en los capítulos anteriores y desentrañar la verdadera contribución de la cubierta vegetal en el control biológico del olivar, se llevó a cabo un análisis de datos obtenidos a una escala espacial y temporal más amplia, correspondientes a distintos olivares de Andalucía durante siete años (Capítulo 7).

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2

Objetivos



Esta tesis doctoral se presenta con el objetivo último de reducir la aplicación de productos químicos de síntesis en olivares mediante la creación de paisajes agrarios funcionales que proporcionen el servicio ecosistémico de control de plagas. Para ello se intenta determinar el efecto de diferentes infraestructuras ecológicas del agroecosistema del olivar en el control biológico por conservación de las plagas de este cultivo. Se plantearon diferentes objetivos específicos que se detallan a continuación:

- Estudiar los posibles efectos conjuntos de cubiertas vegetales y vegetación adyacente al olivar sobre los enemigos naturales.
- Determinar la influencia de distintos tipos de vegetación sobre el control biológico por conservación de las plagas *Prays oleae* y *Euphyllura olivina*.
- Profundizar en el conocimiento de las relaciones entre distintos grupos de enemigos naturales y las plagas *P. oleae* y *E. olivina*.
- Establecer el papel de la cubierta vegetal para el control biológico de plagas del olivo desde un enfoque espacial y temporal amplio.

3

Material y métodos

A landscape photograph showing a field of yellow flowers in the foreground, with several trees and a line of trees in the background under a clear blue sky. The text 'Material y métodos' is overlaid on the lower part of the image.

Los experimentos que se engloban en la presente tesis doctoral han sido llevados a cabo íntegramente en olivares. Para cumplir con los objetivos desarrollados en los capítulos 4, 5 y 6, se dispuso de un olivar experimental. Sin embargo, para el capítulo 7 se utilizaron datos referentes a toda la Comunidad Autónoma de Andalucía proporcionados por la Dirección General de Producción Agrícola y Ganadera y recolectados por la Red de Alerta e Información Fitosanitaria (RAIF), dependiente de la propia Dirección General.

3.1 Áreas de estudio y diseño experimental

3.1.1 Olivar experimental (Capítulos 4, 5 y 6)

El estudio fue llevado a cabo durante los años 2010 y 2011 en una finca experimental de olivar de unas 235 ha., situada en el sur de España, cerca de la ciudad de Granada (37° 17'N y 3° 46'W). Las condiciones climáticas fueron diferentes en los dos años de estudio. La precipitación anual fue superior en 2010 (565,12 mm) que en 2011 (368,82 mm). En 2010 la temperatura media fue inferior (22,1° C) a la de 2011 (24,5° C). La temperatura máxima mensual media desde abril a junio fue de 24,7° C en 2010 y de 27,8° C en 2011.

Esta finca comprende dos zonas adyacentes separadas por una ensenada ocupada por vegetación natural (**Figura 3.1**). En el paisaje que rodea la finca experimental predomina el cultivo de olivar, salpicado de manchas de vegetación natural situadas principalmente en zonas marginales del cultivo y compuestas de especies típicas del bosque mediterráneo. Tres tipos de manchas de vegetación natural adyacente fueron detectadas y catalogadas dentro y cerca de la finca experimental: herbácea, dominada por *Anchusa* sp., *Anacyclus clavatus* Desf. y *Echium plantagineum* L. (**Figura 3.1** y

3.2b); grandes manchas de vegetación leñosa, dominada por árboles, fundamentalmente *Phyllirea angustifolia* L. y *Quercus rotundifolia* Lam., los cuales estaban situados en el barranco que rodea a los olivares (**Figura 3.1** y **3.2c**); y pequeñas manchas de vegetación leñosa, formadas por los arbustos *Genista hirsuta* M. Vahl, *Cistus albidus* L., *Cistus clusii* Dunal y *Rosmarinus officinalis* L., que ocupaban varias decenas de metros cuadrados y estaban localizadas dentro del cultivo en áreas inaccesibles a la maquinaria, usualmente colinas (**Figura 3.1** y **3.2d**).

Las principales plagas que se encuentran en el olivar experimental son la polilla del olivo, *Prays oleae* (Bernard 1788) (Lepidoptera: Yponomeutidae) y el algodoncillo del olivo, *Euphyllura olivina* (Costa 1839) (Hemiptera: Psyllidae). Los grupos de enemigos naturales encontrados más frecuentemente en el olivar experimental son: las arañas (Araneae) destacando entre ellas las familias Thomisidae, Philodromidae, Araneidae, Linyphiidae y Salticidae; las hormigas (Hymenoptera: Formicidae), compuesto fundamentalmente por los géneros *Camponotus*, *Tapinoma* y *Plagiolepis*, los heterópteros depredadores (Homoptera: Heteroptera), conformados por cuatro especies: *Anthocoris nemoralis* (Fabricius 1794), *Deraeocoris punctum* (Rambur 1839), *Pseudoloxops coccineus* (Meyer Dur 1843) y *Brachynotocoris ferreri* n. sp. Baena (in litteris); y los parasitoides (Hymenoptera: Parasitica), los cuales han sido citados o identificados como enemigos naturales de *P. oleae* (Morris et al. 1999), destacando entre ellos las familias Scelionidae, Encyrtidae, Elasmidae y Braconidae. Otros grupos de enemigos naturales, como coccinélidos o el crisópido *Chrysoperla carnea* (Stephens 1836) también estaban presentes en la finca experimental aunque su baja abundancia hizo desestimarlos para algunos de los análisis estadísticos realizados.

Cada zona del olivar experimental fue dividida en dos subzonas, una con suelo desnudo y otra con cubierta vegetal que ocupaba una anchura de 2,5 m entre las calles de los olivos. Dos insecticidas de amplio espectro (glifosato y oxifluorfen) fueron utilizados a principio de la primavera en 2010 y 2011 para eliminar la vegetación y dejar el suelo desnudo. En las subzonas con cubierta vegetal espontánea, las especies vegetales dominantes fueron *Medicago minima* L., *A. clavatus* Desf., *Hordeum leporinum* L., *Lolium rigidum* Gaudich. y *Bromus madritensis* L (**Figura 3.1** y **3.2a**).

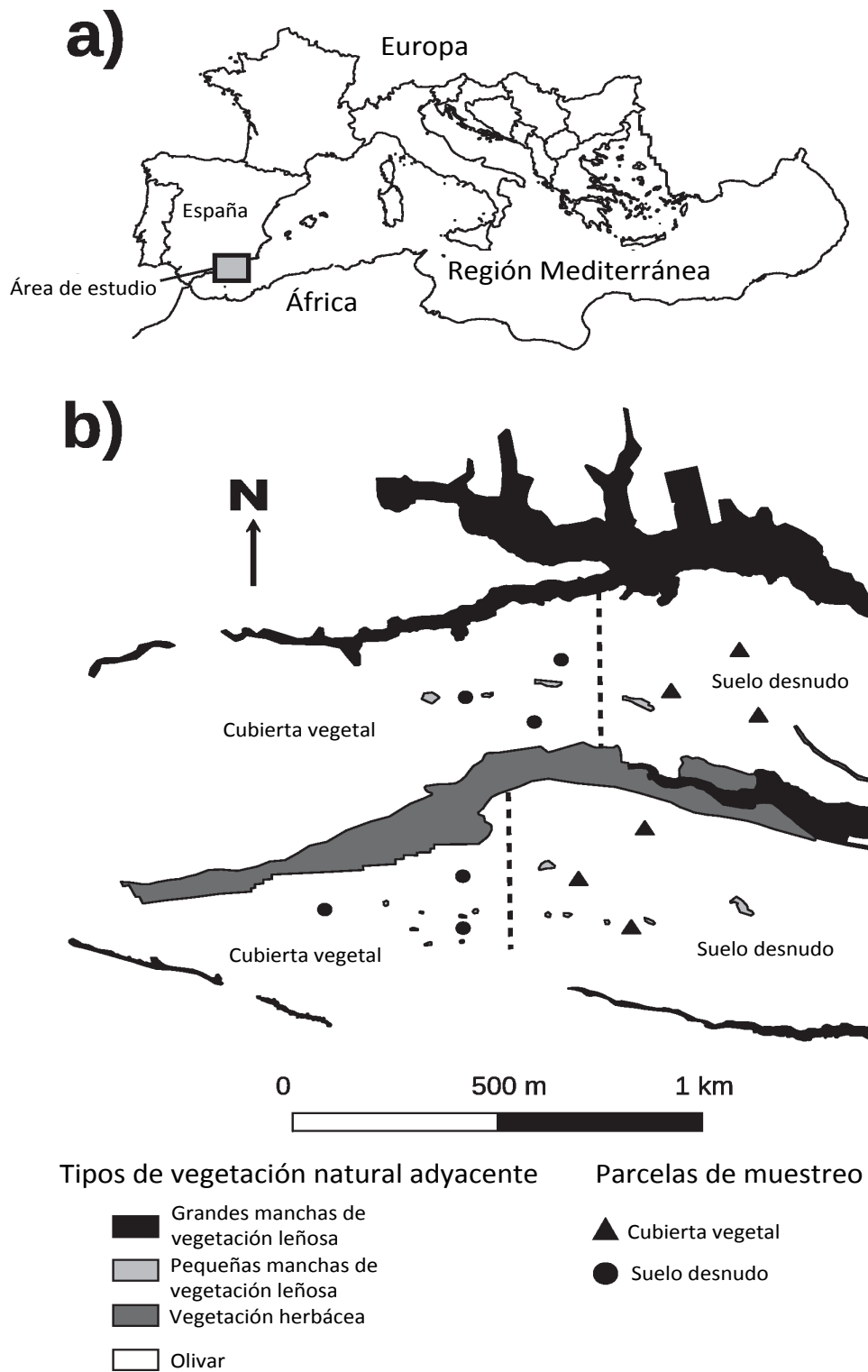


Figura 3.1 Localización y distribución de la finca experimental; a: Localización del área de estudio en el sur de España; b: distribución de la vegetación natural adyacente, las zonas de cubierta vegetal y suelo desnudo en la zona experimental.

La unidad básica de muestreo fue la parcela. Cada una de ellas estaba formada por un cuadrado de 7 x 7 olivos, separados entre sí por una distancia 10 m (4.900 m²). Había un total de 12 parcelas, tres en cada subzona y separadas entre sí unos 150 m (**Figura 3.1**). Los muestreos se realizaron cada 10 días desde finales de marzo a principio de octubre en 2010 y a primeros de julio en 2011. Para cumplir con los distintos objetivos que se plantean en la tesis doctoral, se tomaron diferentes fechas de muestreo por razones que se explicarán en cada capítulo específico. En cada fecha se muestrearon las copas de 16 árboles elegidos al azar en cada parcela, mediante un aspirador G855 durante dos minutos (**Figura 3.3**). Los artrópodos recogidos se almacenaron en hielo para su transporte al laboratorio, donde fueron clasificados.



Figura 3.2 Diferentes infraestructuras ecológicas encontradas en la finca experimental. a: Cubierta vegetal y suelo desnudo; b: Mancha de vegetación herbácea; c: Gran mancha de vegetación leñosa; d: Pequeña mancha de vegetación leñosa.

Los resultados referentes al tratamiento de cubierta vegetal quedan expuestos en los capítulos 4 y 5. Las conclusiones del capítulo 6 son obtenidas mediante el análisis de los datos obtenidos con este muestreo pero aplicando un enfoque estadístico distinto que se explicará en la sección 3.3.1.

3.1.2 Datos de la RAIF

Los datos proporcionados por la Dirección General de Producción Agrícola y Ganadera fueron recolectados por la Red de Alerta e Información Fitosanitaria (RAIF). Esta red se encarga de monitorizar las poblaciones de artrópodos potencialmente dañinos y proporciona orientación a los olivereros sobre como tratar las plagas. Tiene varias estaciones de monitoreo repartidas por toda la región andaluza, cada una cubriendo una superficie de aproximadamente cinco ha. (**Figura 3.4**). Desde 2006, la RAIF ha acumulado gran cantidad de información sobre las plagas del olivo, incluyendo características agronómicas del cultivo.

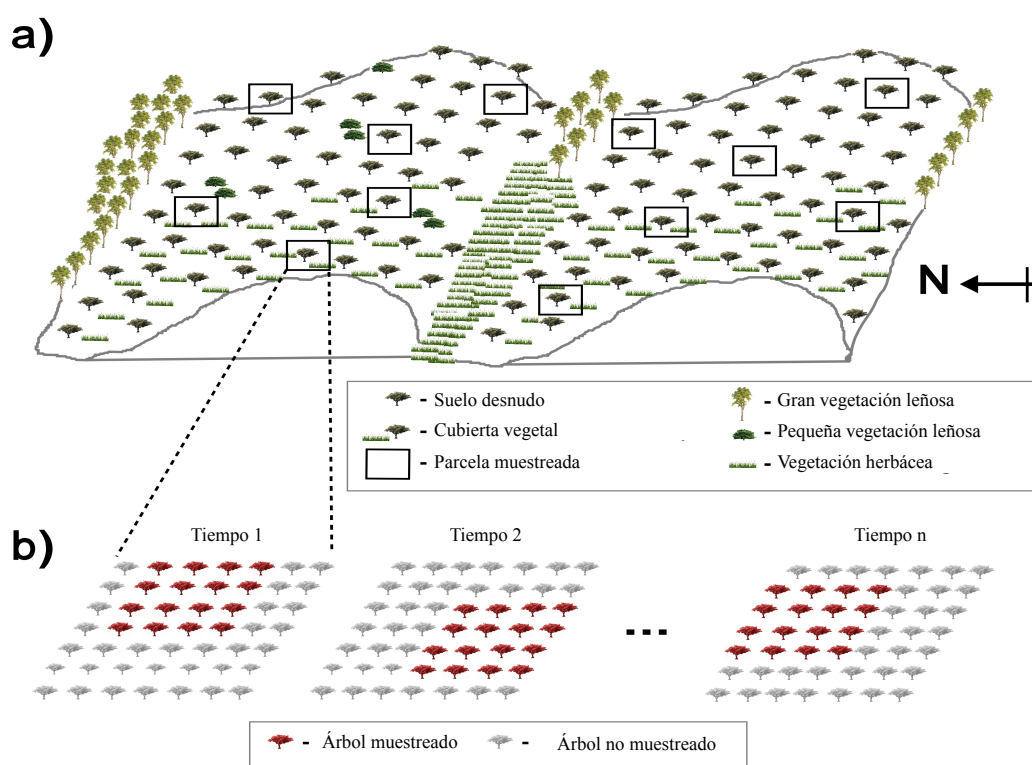


Figura 3.3 a: Representación esquemática del olivar experimental y las diferentes infraestructuras ecológicas (cubierta vegetal, manchas de vegetación herbácea y leñosa); b: Disposición aleatoria de los árboles dentro de la parcela de muestreo.

Al tratarse de un estudio que engloba a toda la región andaluza, todos los artrópodos potencialmente dañinos eran susceptibles de ser analizados. No obstante, y debido principalmente a cuestiones relacionadas con la datos proporcionados, se decidió centrar el estudio en cuatro plagas clave del olivar: *Prays oleae*, *Bactrocera oleae* (Rossi 1790),

Euphyllura olivina, y *Saissetia oleae* (Olivier 1971). De esta forma se analizaron un total de nueve variables respuesta representativas tanto de la abundancia de estas plagas como del daño que éstas producen al olivo, que se explican con más detalle en el capítulo 7 (Tabla 7.1).

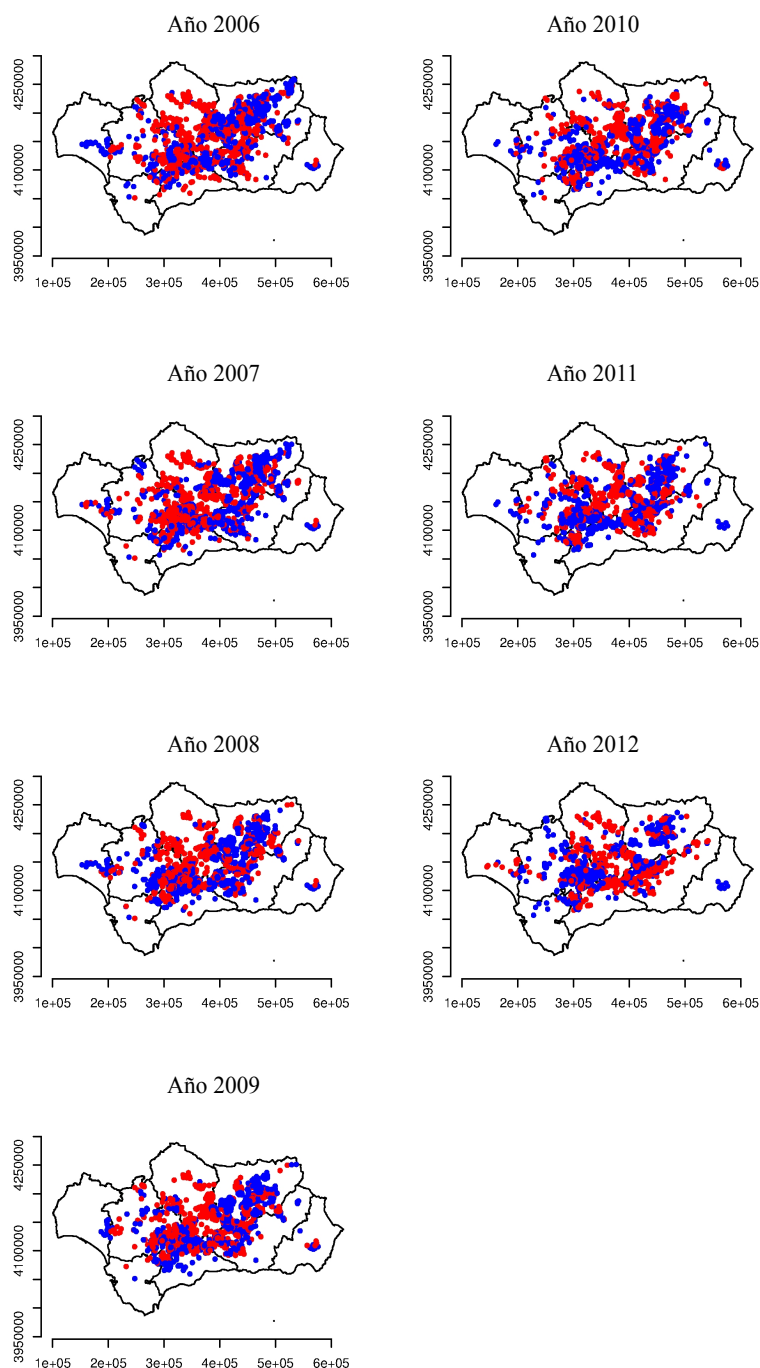


Figura 3.4 Disposición de las diferentes parcelas de muestreo (puntos azules: cubierta vegetal, puntos rojos: suelo desnudo) en la región andaluza.

3.2 Descripción de las principales especies plaga

3.2.1 Prays oleae

Es una plaga importante del olivo en la cuenca mediterránea. El daño causado por ella puede reducir la producción en un 50-60%, lo cual equivale a 8-11 kg por árbol y año en olivares modernos (Ramos et al. 1998). Tiene tres generaciones: filófaga, antófaga y carpófaga. Las dos últimas son las más dañinas. Las larvas de la generación antófaga se alimentan de los botones florales, reduciendo drásticamente la formación potencial de fruto. La larva de la generación carpófaga se desarrolla dentro del hueso de la aceituna y causa la caída prematura del mismo, reduciendo así la productividad del cultivo.

3.2.2 Bactrocera oleae

La mosca del olivo es considerada como la plaga más dañina del olivo. Este insecto oviposita en el mesocarpo de la aceituna, donde la larva desarrolla tres estadios (Arambourg 1986). Dependiendo de las condiciones ambientales puede presentar de una a tres generaciones desde julio hasta finales del otoño, siendo la más dañina la que ocurre en otoño. La larva orada las aceitunas, provocando su caída. El daño puede ser muy grande, llegando en algunos años a la pérdida total de la producción.

3.2.3 Euphyllura olivina

Es una plaga muy importante en el Norte de África (Jarraya 2004). En países europeos mediterráneos está considerada como una plaga secundaria, pero se podría convertir en una seria amenaza en un contexto de cambio climático (Malumphy 2011). Las ninfas de este insecto atacan los brotes jóvenes y las inflorescencias, pudiendo causar en éstas daños de hasta el 70% (Jarraya 2004).

3.2.4 Saissetia oleae

Se encuentra ampliamente distribuida y ataca varios árboles frutales. Esta plaga infesta las hojas y ramitas del olivo, succiona la savia del árbol y produce grandes cantidades de melaza, la cual sirve de sustrato para el hongo del moho negro. Este hongo interfiere con los procesos respiratorios y fotosintéticos del olivo. Como consecuencia se produce una pérdida de la producción y de la calidad de la aceituna (Argov y Rössler 1993).

3.3 Análisis de datos

Para cumplir con los diferentes objetivos específicos incluidos en la presente tesis doctoral, se utilizaron tres aproximaciones metodológicas: uso de modelos gaussianos (Capítulos 4 y 5), uso de técnicas correlacionales (Capítulo 6) y uso de modelos lineales generalizados mixtos (Capítulo 7). Siempre que se usaron modelos se optó por la utilización de métodos de selección de modelos en lugar del tradicional contraste de hipótesis (Johnson y Omland 2004; Canham y Uriarte 2006). Este método se basa en la selección del modelo o modelos más parsimoniosos dentro de un conjunto de modelos plausibles. Para determinar la parsimonia de los modelos se utilizan diferentes criterios de información. En nuestro caso la comparación se llevo a cabo con el criterio de información Akaike (AIC). El modelo con un valor de AIC menor es considerado el más parsimonioso. Se estableció un valor de dos como el umbral del soporte virtual del modelos, es decir, diferencias de $AIC > 2$ entre dos modelos desestimaban el de mayor dato para extraer conclusiones. Para los capítulos 4 y 5 se aplicó un factor de corrección para muestras pequeñas (Burham y Anderson 2002). Todos los análisis fueron desarrollados bajo el ambiente R (R Development Core Team 2012)

3.3.1 Modelos gaussianos

El efecto de las infraestructuras ecológicas en los enemigos naturales (Capítulo 4) y en las plagas (Capítulo 5) fue analizado mediante métodos de máxima verosimilitud

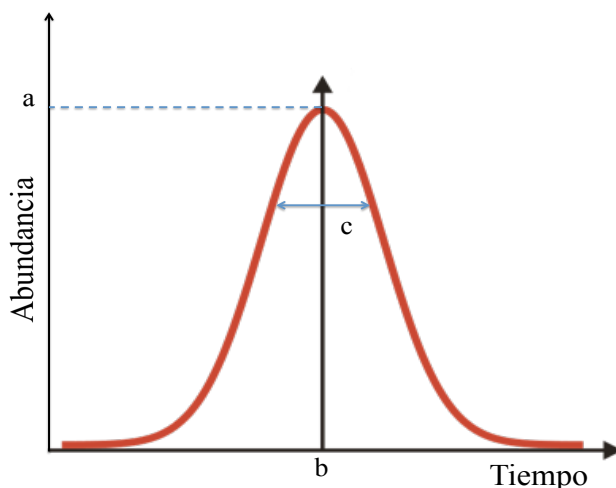


Figura 3.5 Representación gráfica de la función gaussiana.

El efecto de las infraestructuras ecológicas en los enemigos naturales (Capítulo 4) y en las plagas (Capítulo 5) fue analizado mediante métodos de máxima verosimilitud (Canham y Uriarte 2006; Gómez-Aparicio et al. 2013). Se optó por una función gaussiana para modelar la abundancia tanto de enemigos naturales (Capítulo 4) como de plagas (capítulo 5) en función del tiempo (Ecuación 3.1). La representación de esta función describe el comportamiento típico de las poblaciones de artrópodos, los cuales presentan un periodo de crecimiento alcanzando un máximo para decrecer después. La curva gaussiana es una curva simétrica con forma de campana definida por tres parámetros: a , b y c (**Figura**

3.5). El parámetro a es la altura de la curva, en nuestro caso, la máxima abundancia que los artrópodos pueden alcanzar. El punto del tiempo en que la curva alcanza su máximo está representado por el parámetro b , el cual está contabilizado en días a partir del 1 de enero. El parámetro c representa la desviación estándar de la curva y controla la anchura de la misma (**Figura 3.5**; Ecuación 1). Se compararon varios modelos en donde los distintos parámetros de la función gaussiana variaron en respuesta a la existencia de cubierta vegetal, la vegetación circundante y el año. De esta forma el mejor modelo seleccionado por los procedimientos ya descritos (ej. criterios de información) permitirá inferir el efecto de distintas infraestructuras ecológicas sobre el ciclo de las especies estudiadas. Se utilizó un procedimiento de optimización global (*simulated annealing*) para determinar los parámetros más adecuados de acuerdo con los datos observados (Goffe et al. 1994). Una estructura de errores de tipo Poisson fue utilizada para todas las variables respuesta (plagas y enemigos naturales). La R^2 del ajuste del modelo (1-SSE/SST; error de la suma de cuadrados (SSE) error de la suma total (SST)) de datos observados contra los predichos fue usada como medida de la bondad de ajuste del modelo. Todos los análisis fueron llevados a cabo con el paquete “likelihood” (Murphy 2012).

$$Abundancia = a \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Ecuación 3.1}$$

3.4.2 Métodos correlacionales

Para profundizar en el conocimiento de las relaciones entre distintos grupos de enemigos naturales y las plagas *P. oleae* y *E. olivina* se optó por el uso de métodos correlacionales. Este tipo de técnica estadística es incompatible con la identificación de relaciones causa efecto por lo que las conclusiones relativas deben tenerse en cuenta a modo de posibles procesos que deben ser analizados específicamente. Se utilizaron correlaciones de Pearson para explorar la relación entre la abundancia de pares de enemigos naturales. Además, se llevó a cabo un escalamiento multidimensional no métrico (NMDS, por sus siglas en inglés), una técnica de ordenación basada en matrices de distancias, para investigar el patrón general de composición de especies en los posibles conjuntos de depredadores (enemigos naturales) que pudiesen responder de manera similar a condiciones ambientales, estructuras de hábitat y

disponibilidad de recursos. La distancia de disimilitud de Bray-Curtis fue utilizada para calcular la matriz de similitud entre parcelas. Para explorar asociaciones entre determinadas especies de depredadores o conjuntos de los mismos y las plagas se generaron superficies suavizadas para las dos especies plaga en el diagrama de ordenación del escalamiento multidimensional no métrico. Las superficies suavizadas son el resultado de ajustar las predicciones de modelos generales aditivos (GAM) sobre la representación del NMDS interpolándolas como líneas (Oksanen et al. 2012). Todos los análisis fueron llevados a cabo con el paquete “vegan” de R (Oksanen et al. 2012).

3.3.3 *Uso de modelos lineales generalizados mixtos*

Para el capítulo 7 también se utilizó la selección de modelos, pero dada la naturaleza de los datos, se optó por ajustar modelos lineales mixtos generalizados (GLMM). Los modelos lineales mixtos generalizados permiten analizar datos que se encuentran correlacionados o anidados en una estructura jerárquica, atribuyendo una variabilidad aleatoria a cada uno de los niveles que constituyen esta estructura (Zuur et al. 2009). De esta forma el modelo estima la variabilidad explicada por efectos fijos, normalmente los tratamientos que se quieren evaluar, y por efectos aleatorios, típicamente aquellos derivados de la propia naturaleza del diseño experimental utilizado. Este tipo de modelos son muy versátiles ya que además admiten diversas distribuciones de errores: gaussiana, Poisson o binomial, las cuales vienen determinadas por la naturaleza de la variable respuesta. Siguiendo Nakagawa y Schielzeth (2012), calculamos la R^2 de los mejores modelos para tener un dato acerca de la cantidad de variabilidad explicada por el modelo. Estos autores también incluyen dos medidas de este parámetro: (1) un R^2 marginal (R_m^2), que sólo tiene en cuenta la variabilidad explicada por los efectos fijos; y (2) un R^2 condicional (R_c^2), que tiene en consideración la variabilidad explicada por los efectos fijos y los aleatorios. Todos los análisis fueron llevados a cabo con el paquete “lme4” (Bates et al. 2013) y “MuMIn” (Barton et al. 2013).

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A close-up photograph of an olive branch with several olives in various stages of ripeness, from green to purple. The leaves are elongated and green. The background is a blurred green field.

4

**Synergistic effects of ground cover
and adjacent vegetation on natural
enemies of olive insect pests**

Summary

The use of pesticides in conventional agriculture poses several risks to humans and to the environment, and may turn out to be inefficient in the long-term as pests can develop resistance to pesticides. Non-chemical control methods can be preferable to prevent pest damage. One way to achieve this involves the establishment of ground cover or the restoration of vegetation adjacent to the crop. Either of these methods can effectively increase the abundance of natural enemies, particularly in perennial crops, but their interaction has been typically neglected. In this study we used maximum likelihood methods to analyse the synergistic effects of ground cover and different types of adjacent vegetation (herbaceous, woody) on the abundance of the main natural enemy groups of insect pests in olive groves. A Gaussian function was used to predict their abundance as a response of time, ground cover, different types of adjacent vegetation and year (2010, 2011). We examined 40 different alternative models for each group of natural enemies: spiders, ants, predatory Heteroptera, and parasitoids. Spiders, parasitoids, and one species of predatory Heteroptera (*Deraeocoris punctum*), showed a greater abundance in ground cover plots. Overall, herbaceous and large woody vegetation adjacent to the crop influenced the abundance of natural enemies more than small woody vegetation. However, this effect was modulated by ground cover. When both structures were present in the crop, the abundance of some groups of natural enemies (spider and parasitoids) was positively influenced by adjacent vegetation, whereas this effect was lower or even reversed in bare soil crops. We thus encourage olive farmers to use both habitat management approaches simultaneously, since the interaction of these ecological infrastructures produce an effect that maximizes the abundance of natural enemies.

Este capítulo reproduce íntegramente el siguiente artículo:

Paredes D, Cayuela L, Campos M. 2013. Synergistic effects of ground cover and adjacent natural vegetation on natural enemies of olive insect pests. *Agriculture, Ecosystems and Environment* 173: 72-80.

4.1 Introduction

Olive culture is of great importance in the circum-Mediterranean region. Olive crops occupy ca. 7.6 million hectares, of which 2.5 million hectares are in Spain, the main olive oil producer and exporter. In 2012 alone, this crop yielded approximately 1.5 million tons of olive oil in Spain. Conventional production practices are based on the use of fertilizers, herbicides and pesticides. This has led to important environmental problems, such as the loss of natural vegetation and bare soil due to herbicide use, which can cause erosion and loss of natural soil fertility (Metzidakis et al. 2008). To avoid some of these problems, new policies are currently being implemented in the European Union, aiming at the restoration of adjacent natural vegetation and the establishment and maintenance of ground cover (IOBC 2012).

Vegetation adjacent to the crop (henceforth natural vegetation) has been shown to be an efficient tool to enhance the abundance and diversity of natural enemies (Altieri and Letourneau 1982; Bianchi et al. 2006; Griffiths et al. 2008; Thomson and Hoffmann 2009). This in turn can translate into decreased crop damage in adjacent crops and could provide direct benefits by reducing the use of costly pesticides (Tschardt et al. 2002; Tsitsilas et al. 2006) and associated environmental and human health concerns (Meehan et al. 2011). Herbaceous and woody vegetation patches interspersed within the crop, or located at the crop margins mainly form this natural vegetation (Bianchi et al. 2006). Overall, these structures are very important for the establishment and survival of arthropods (Thies and Tschardt 1999), since they can provide food resources such as nectar, pollen or alternative prey, and shelter when the crop is disturbed (Landis et al. 2000). Therefore, they have been used to increase natural enemy efficiency in order to reduce the incidence of crop pests (Scheid et al. 2011; Simpson et al. 2011).

In perennial crops, the use of natural or planted ground cover vegetation can also contribute to an increase in the abundance of natural enemies, in addition to reduced soil erosion. Ground cover has been reported to increase the abundance of different groups of natural enemies (Smith et al. 1996; Rieux et al. 1999; Danne et al. 2010; Silva et al. 2010) but in some studies this increase has not been reported (Costello and Daane 1998; Bone et al. 2009). Most of these studies, however, have systematically neglected the role of natural vegetation interspersed within or near the crop, thus ignoring the possibility of synergistic effects between ground cover and natural vegetation (but see Woltz et al. (2012) for a case study in soybean fields).

We hypothesised that populations of natural enemies within the olive grove may be affected by adjacent natural vegetation, and their response might differ depending on the presence of ground cover within the crop. We therefore aimed to: (i) establish the effect that ground cover, as compared to bare soil areas, has on the abundance of natural enemies in olive groves; (ii) determine the influence of different types of adjacent natural vegetation on their abundance; and (iii) identify potential synergistic effects between ground cover and different types of adjacent natural vegetation.

The results of this study will contribute to a deeper understanding of the interactions between arthropods, ground cover and adjacent vegetation, and will provide mechanisms to improve the biological control of pest outbreaks in so widespread and socially important crop such as olive orchards, while reducing environmental and production costs by avoiding (or minimising) the use of chemical products.

4.2 Material and methods

4.2.1 Study area

The study was conducted in an experimental olive grove (235 ha) located in southern Spain, near the city of Granada (37°17'N and 3°46'W). It comprised two adjacent zones separated from each other by a creek occupied by natural vegetation (**Figure 3.1**). The topographical conditions were typical from the olive groves in the region. Climatic conditions were different in both years. Average annual precipitation was higher in 2010 (565.12 mm) than in 2011 (368.82 mm). In 2010 mean average temperature was lower (22.1°C) than in 2011 (24.5°C). Average maximum monthly temperature from April to June was 24.7°C in 2010 and 27.8°C in 2011. The main insect pests in this area

were the olive moth *Prays oleae* Bern. (Lepidoptera: Plutellidae), and the olive psyllid *Euphyllura olivina* Costa (Hemiptera: Psyllidae). Both are widely distributed in the circum-Mediterranean region and often cause costly damage to crops by reducing the number and/or size of the fruits, with a subsequent reduction in the yield and quality of the resulting fruit or oil (Tzanakakis 2006). Four main natural enemies groups were considered: spiders (Araneae), ants (Hymenoptera: Formicidae), predatory Heteroptera (Hemiptera: Heteroptera) and parasitoids (Hymenoptera: Parasitica). Most of these groups have been reported as natural enemies of *P. oleae* (Morris et al. 1999).

Three different types of adjacent natural vegetation patches were found in and near the crop, namely herbaceous, large and small woody vegetation patches. Herbaceous vegetation was dominated by *Anchusa* sp., *Anacyclus clavatus* and *Echium plantagineum*. Woody vegetation patches were divided into two groups namely large woody patches, dominated by trees which occupied the ravines surrounding the grove, and small woody patches, formed by shrubs occupying no more than a few square meters and located inside the grove, usually at hilltops, in areas inaccessible to machinery (**Figure 3.1**). Large woody patches were dominated by *Phyllirea angustifolia* and *Quercus rotundifolia*, whereas small woody patches were mainly composed by *Genista hirsuta*, *Cistus albidus*, *Cistus clusii*, and *Rosmarinus officinalis*.

4.2.2 Experimental design and sampling

Each zone within the grove was divided into two subzones, each one occupied by either bare soil or ground cover, respectively. Two broad spectrum herbicides (glyphosate and oxyfluorfen) were sprayed in the bare soil subzones in early spring 2010 and 2011 to remove weeds. In subzones with ground cover, spontaneous herbaceous vegetation was allowed to grow in a 2.5 m wide strip between tree lines. The remaining area between trees was treated with the same herbicides as for bare soil. No insecticides were used in the grove for two years throughout of the experiment. Ground cover was composed of herbaceous plants dominated by *Medicago minima*, *Anacyclus clavatus*, *Hordeum leporinum*, *Lolium rigidum*, and *Bromus madritensis*.

The basic experimental unit in our study was the plot. There were a total of twelve plots, three in each subzone, which were sampled in different dates (**Figure 3.1**). Plots were located equidistant from each other in the two zones and subzones. Each plot had a

square shape comprising 7x7 olive trees and an area of 4900 m², as olive trees are 10 m apart from all other adjacent olive trees. Within each plot, a square of 4x4 olive trees was randomly selected at each date, corresponding to an area of 1600 m². Samples were collected every ten days, weather allowing, from late March to early October in 2010 and from early April to early July in 2011. Overall, there were 20 sampling dates in 2010 and nine sampling dates in 2011. A modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, Florida, USA) was used for two minutes to trap the arthropods in the canopy of each of the 16 olive trees (**Figure 3.3**). Once the arthropods were collected, they were stored on ice for transportation to the laboratory where they were classified. Parasitoids and spiders were determined to family level, ants were determined to genus level, and predatory Heteroptera to species level. Other groups of natural enemies, such as crisopids and coccinelids, were also collected but in low abundance, so they were not considered in this study. Phytophagous insects were determined to species level but analysed separately in the next chapter. Samples from all 16 trees in each plot and date were pooled together to obtain a measure of abundance for each group of natural enemies.

4.2.3 Other explanatory variables

We digitalised all patches of natural vegetation using aerial photographs, and a 1x1 m resolution grid was superimposed upon the resulting vector maps. A bivariate Gaussian kernel density function (Diggle 1985) was computed from the 1x1 m grid and its value was calculated for each plot in order to obtain a distance weighted measure of the influence of each natural vegetation type on that plot. A standard deviation of 120 m was chosen for the gaussian kernel density function, as Miliczky and Horton (2005) reported this as the maximum distance of dispersal of some groups of natural enemies in orchards. Other studies have reported even minimum distances of dispersal: 100 m for parasitoids and 50 m for spiders in vineyards (Thomson and Hoffman 2009); 60 m for arthropods in winter wheat crop (Holland et al. 2004); and 58 m for generalist predators of beetles in cereal crops (Collins et al. 2002). This measure also allowed incorporating the influence of vegetation at distances further than 120 m by assigning progressively lower weights, by means of the Gaussian density function, as we moved away from the plot. These analyses were performed with the R package 'spatstat' (Baddeley and Turner 2005).

Because we conducted our study throughout two consecutive years, we also included year, a factor with two levels (2010, 2011), as an explanatory variable in the models. Differences between years are assumed to occur as a direct response of arthropod abundance to changes in climatic conditions and other non-measured variables that display inter-annual variability.

4.2.4 Data analysis

We used a gaussian function to describe the predicted abundance of the main groups of natural enemies in response to time, since these groups typically show an increase in abundance during spring, reaching a maximum and declining afterwards. The gaussian curve is a characteristic symmetric "bell curve" shape defined by three parameters: a , b and c . Parameter a is the height of the curve's peak; in our case, the maximum abundance that a certain group could reach. The point in time when the highest abundance is reached is represented by parameter b , which is days since the first of January, and represents the mean of the gaussian curve. Parameter c represents the standard deviation and controls the width of the "bell". Our *basic model* is represented by the equation below:

$$Abundance = a \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Equation 4.1}$$

where X is time, measured in Julian days since the first of January. Note that the account of days restarts every year.

The basic gaussian function was modified to account for differences in the estimated parameters across treatments (ground cover and bare soil; parameter a) and years (2010, 2011; parameters a , b , c), as well as to incorporate the effect of different types of natural vegetation on the estimated curve's peak (parameter a). We used likelihood methods and model selection as an alternative to traditional hypothesis testing (Johnson and Omland 2004; Canham and Uriarte 2006), for data analysis. Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the abundance measured in the field, given a suite of alternative models.

Overall, we examined 40 different alternative models for each group of natural enemies and for their most representative lower taxonomic division.

The basic model was modified in order to allow the maximum abundance (a) to vary between treatments (bare soil, ground cover). Such models will be referred to henceforth as *ground cover models* (Equation 4.2).

$$Abundance = a_j \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Equation 4.2}$$

where a_j represents the maximum abundance of natural enemy groups in each treatment (j).

Equations 4.1 and 4.2 were further modified to include the effect of natural vegetation density. The effect of each type of natural vegetation (herbaceous, large woody and small woody patches) on parameter a was modelled separately by adding a set of new parameters ($d.herb$, $d.lwp$, $d.swp$). This is reflected by:

$$Abundance = (a + \gamma) \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Equation 4.3 (extension of basic model)}$$

$$Abundance = (a_j + \gamma) \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Equation 4.4 (extension of ground cover model)}$$

$$\gamma = (d.herb \cdot X_{herb} + d.lwp \cdot X_{lwp} + d.swp \cdot X_{swp}) \quad \text{Equation 4.5}$$

where γ represents the effect of natural vegetation patches on the maximum abundance of natural enemy groups, as expressed by parameters $d.herb$, $d.lwp$, and $d.swp$, which can be positive or negative. X_{herb} , X_{lwp} , and X_{swp} are the values of the kernel density function at each plot for herbaceous, large, and small woody vegetation patches respectively. A positive or negative effect of the natural vegetation represents contribution to (source vegetation patches) or removal from (sink vegetation patches) the grove, respectively (Duelli et al. 1990).

A variation of equation 4.4 would be that in which the effect of different types of natural vegetation patches on the abundance of natural enemy groups is allowed to vary between bare soil and ground cover plots. Such effects can be regarded as an interaction between natural vegetation density and treatment. This model is described by equation:

$$Abundance = (a_j + \gamma_j) \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Equation 4.6}$$

$$\gamma_j = (d.herb_j \cdot Xherb + d.lwp_j \cdot Xlwp + d.swp_j \cdot Xswp) \quad \text{Equation 4.7}$$

where γ_j represents the effect of natural vegetation patches on the maximum abundance of natural enemy groups in each treatment (j), which results from multiplying parameters $d.herb_j$, $d.lwp_j$ and $d.swp_j$, estimated separately for bare soil and ground cover, by the observed values of herbaceous ($Xherb$), large ($Xlwp$) and small woody patch ($Xswp$) densities, respectively.

Inter-annual climatic variability could also influence the shape of the abundance response curve. Such an effect was included in former models (Equations 4.1, 4.2, 4.3, 4.4 and 4.6) by allowing all possible combinations of parameters a , b and/or c to vary between years. The basic model allowing all three parameters to vary between years is expressed as:

$$Abundance = a_i \cdot \exp\left(-\left(\frac{(x-b_i)^2}{2c_i^2}\right)\right) \quad \text{Equation 4.8}$$

where a_i , b_i and c_i represent maximum abundance, mean and standard deviation of the gaussian curve in year i .

Therefore, the most complex model, taking into account the effects of ground cover (Equation 4.2), natural vegetation (Equations 4.3, 4.4), the interaction between these two (Equation 4.6), and inter-annual variability (Equation 4.8), can be expressed as:

$$Abundance = (a_{ij} + \gamma_j) \cdot \exp\left(-\left(\frac{(x - b_i)^2}{2c_i^2}\right)\right) \quad \text{Equation 4.9}$$

We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e. the parameters that maximize the log-likelihood) given our observed data (Goffe et al. 1994). We used a Poisson error structure for all response variables. Alternative models were compared using the Akaike Information Criterion (AIC_c) corrected for small sample size (Burnham and Anderson 2002). Models with a difference in AIC_c > 2 indicate that the worse model has virtually no support and can be omitted from further consideration. We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). The R^2 of the model fit ($1 - \text{SSE}/\text{SST}$, sum of squares error (SSE) sum of squares total (SST)) of observed versus predicted was used as a measure of goodness-of-fit. All analyses were performed using the 'likelihood' package (Murphy 2008) written for the R environment (R Development Core Team 2012).

4.3 Results

A total of 47,938 arthropods were trapped during the two years of the study. Of these, 5,842 were spiders, 5,025 were ants, 14,651 were predatory Heteropterans, and 22,420 were parasitoids. Comparison of alternative models revealed those that best fit the different response variables (**Table 4.1**). The resulting estimated parameters are shown in **Table 4.2**. A detailed account of the results for each group of natural enemies follows.

4.3.1 Spiders

The best fit model for spiders was found in the ground cover model, with differential effects of adjacent natural vegetation on bare soil and ground cover plots, and an effect of inter-annual variability on parameters b and c (AIC_c= 2648.93, $R^2=0.72$; **Table 4.1**). The peak of abundance was notably higher in ground cover (45 spiders/plot) than in bare soil plots (35 spiders/plot) (parameter a ; **Table 4.2**). The timing of the highest abundance and the width of the bell differed between years (parameters b and c respectively; **Table 4.2**).

Figure 4.1a summarises the effects of different types of natural vegetation on spider abundance. A negative effect of herbaceous vegetation was found in both bare soil and ground cover plots (parameter *d.herb*; **Table 4.2**). Large woody vegetation patches had a positive effect on spider abundance in ground cover plots and a negative effect in bare soil plots (parameter *d.lwp*; **Table 4.2**). Small woody vegetation patches always had a positive effect on spider abundance, but this effect was almost threefold in ground cover plots than in bare soil plots (parameter *d.swp*; **Table 4.2**). Patches that displayed a positive effect (mostly large woody vegetation, **Figure 4.1**) remarkably increased spider abundance in ground cover plots, whereas this increase was less marked in bare soil plots (**Figure 4.2**).

Table 4.1 Comparison of alternative models (using AIC_c) for the main arthropod natural enemy groups of insect pests in olive groves.

			AIC _c			
			Spiders	Ants	Predatory Heteroptera	Parasitoids
Basic model	No vegetation effect	General response	3093.54	7630.75	7978.57	19770.85
		Inter-annual variability	2999.24	7481.92	6491.16	18952.05
	Natural vegetation effect	General response	2943.26	7175.32	7834.13	17926.85
		Inter-annual variability	2849.77	7050.85	6341.28	17102.88
Ground cover model	No vegetation effect	General response	2838.93	7534.68	7871.95	18015.22
		Inter-annual variability	2750.40	7429.08	6786.72	17318.42
	Natural vegetation effect	General response	2740.33	7169.50	7743.02	17090.14
		Inter-annual variability	2651.92	7064.01	6545.10	16393.45
	Natural vegetation effect x ground cover	General response	2737.32	6666.36	7645.18	16860.08
		Inter-annual variability	2648.93	6560.82	6734.16	16163.60
		R ²	0.72	0.14	0.63	0.59
		Number of Parameters	12	12	9	12

The best model (lowest AIC_c) is indicated in boldface type. The number of parameters and R² refer to the best model. For brevity, we have presented in Table 1 only the most parsimonious (i.e. lowest AIC_c) of all possible models that include inter-annual variability with one, two or three parameters varying between years.

The models did not explain differences in abundance for the most representative spider families in the study area (Linyphiidae, $R^2= 0.42$; Thomisidae, $R^2= 0.40$; Salticidae, $R^2=0.32$; **Table 4.3** and **4.4**) to the extent it did for all spider families together ($R^2=0.72$; **Table 4.1**).

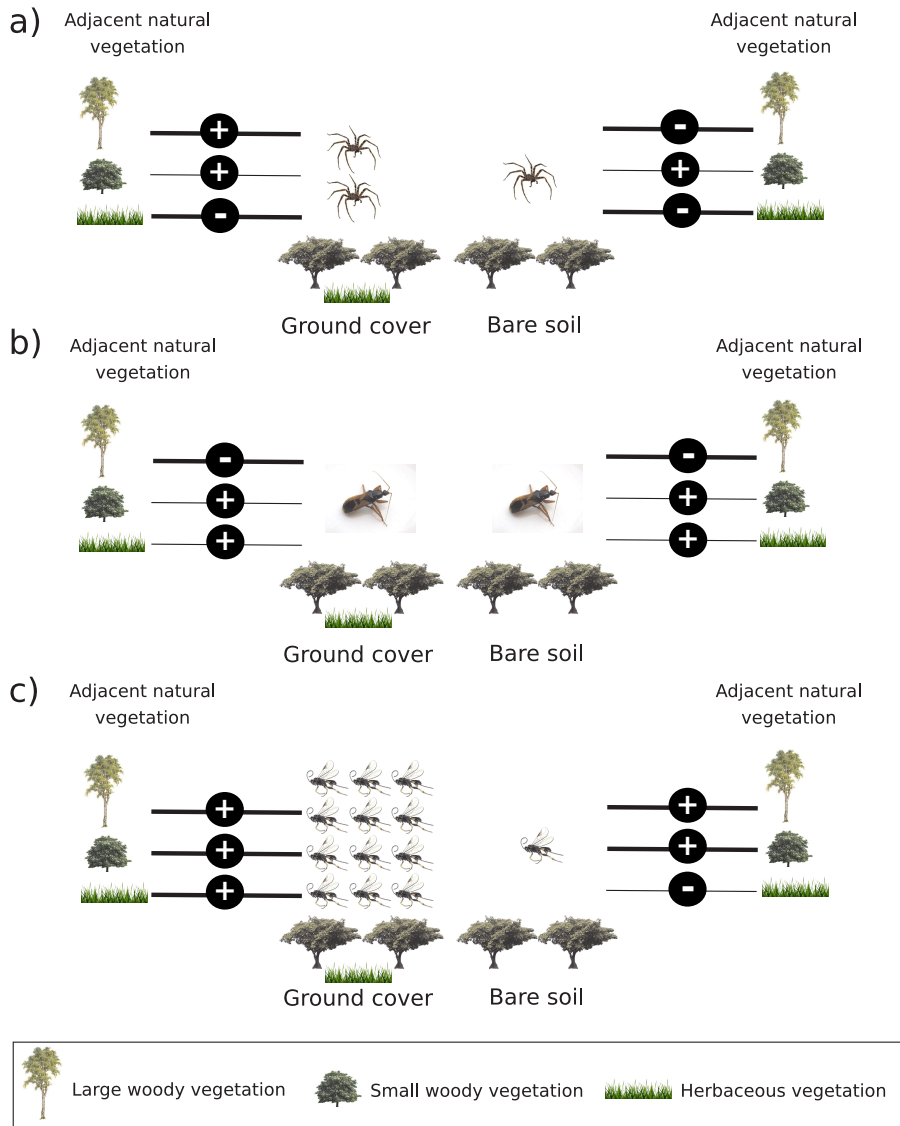


Figure 4.1 Schematic representations of the main effects of ground cover (as compared to bare soil) and different types of natural vegetation. a: Spiders; b: Predatory Heteroptera; and c: Parasitoids. Thick arrows indicate the most important effects based on estimated coefficients (**Table 4.2**) and model predictions (see **Figure 4.2**). The number of spiders, predatory Heteroptera and parasitoids represent an estimation of the relative effect of ground cover as compared to bare soil (**Table 4.2**).

4.3.2 Ants

The best model for ants resembled that of spiders, but with a poorer fit ($AIC_c = 6560.82$, $R^2 = 0.14$; **Table 4.1**). Therefore, we did not show the resulting estimated parameters for this group nor figures summarising the effects of different types of natural vegetation on its abundance.

Table 4.2 Parameter estimates for the most parsimonious models of abundance of the natural enemy.

	Spiders	Predatory Heteroptera	Parasitoids
a			
Ground cover	45 [44; 46]		109 [105; 113]
Bare soil	35 [34; 36]		$1.37e^{-9}$ [$1e^{-19}$; 3]
2010		114 [111; 116]	
2011		80 [78; 82]	
b			
2010	256	183	176
2011	303 [300; 306]	153	166
c			
2010	0.0148 [0.0145; 0.0150]	0.0311 [0.0308; 0.0314]	0.0491 [0.0486; 0.0496]
2011	0.0092 [0.0091; 0.0094]	0.0334 [0.0327; 0.0340]	0.0560 [0.0554; 0.0565]
d.herb			
Ground cover	-1141.07 [-1444.25; -829.30]		16036.72 [14950.03; 17038.72]
Bare soil	-1364.83 [-1736.01; 987.83]		-3205.95 [-4538.29; -2090.41]
d.lwp			
Ground cover		-8929.13 [-10136.18; -7892.41]	
Bare soil	2436.06 [1182.47; 3655.55]		70800.20 [66676.20; 75508.18]
	-3272.75 [-4137.77; -2447.16]		76656.36 [74356.67; 78656.34]
d.swp			
Ground cover		5729.09 [2499.92; 8860.34]	
Bare soil	3120.14 [232.78; 5957.58]		178297.50 [169165.60; 188297.40]
	981.87 [-2077.60; 4021.64]		294220.30 [283393.70; 303046.90]

Parameter *a* is the maximum abundance of natural enemy groups in each treatment (ground cover, bare soil) and year (2010, 2011); *b* and *c* represent the mean and standard deviation of the gaussian curve in different years. The parameters *d.herb*, *d.lwp* and *d.swp* (herbaceous, large and small woody vegetation respectively) represent the effect of adjacent natural vegetation on the maximum abundance of natural enemy groups in bare soil and ground cover plots. Two-unit support intervals in brackets.

4.3.3 Predatory Heteroptera

The best-fit model for predatory Heteroptera only included the effect of natural vegetation and inter-annual variability on the abundance of this group ($AIC_c = 6341.28$, $R^2 = 0.63$; **Table 4.1**). The peak of abundance was higher in 2010 (114 predatory Heteroptera/ plot) than in 2011 (80 predatory Heteroptera/ plot) (parameter *a*; **Table 4.2**). The point when the maximum abundance was reached and the width of the bell also differed between years (parameters *b* and *c* respectively; **Table 4.2**).

Figure 4.1b summarises the effects of different types of natural vegetation on the abundance of predatory Heteroptera. Herbaceous vegetation and small woody vegetation patches displayed a positive effect on

heteropteran abundance (parameters *d.herb* and *d.swp* respectively; **Table 4.2**) whereas the effect of large woody vegetation patches was negative (parameter *d.lwp*; **Table 4.2**). Overall, patches that displayed a negative effect (i.e. large woody vegetation; **Figure 4.1**) exerted a more marked influence on the abundance of this group than patches that displayed a positive effect (small woody and herbaceous; **Figure 4.2**).

At species level (**Table 4.3**), the best-fit models for three of the most abundant heteropteran species were similar to that found for the main group (**Table 4.4**), with differences in the effects of different types of natural vegetation (**Table 4.5**). Two of these three species, *Pseudoloxops coccineus* and *Brachynotocoris ferreri* showed a very good-fit ($R^2 = 0.84$ and $R^2 = 0.73$; **Table 4.4**), whereas *Anthocoris nemoralis* did not show such a good-fit as the other species ($R^2 = 0.38$; **Table 4.4**). The same poor-fit ($R^2 = 0.38$; **Table 4.4**) was found for *Deraeocoris punctum*, but in this particular case the best fit model included a positive effect of ground cover, differential effects of adjacent natural vegetation between bare soil and ground cover plots, and differences between years (**Table 4.5**).

Table 4.3 Relative abundance of each taxon within the main arthropod natural enemy groups found in the experimental olive grove.

		Relative abundance (%)	
		2010	2011
Spiders		15.91	6.91
	Linyphiidae	34.62	42.27
	Thomisidae	15.47	9.72
	Salticidae	13.35	14.07
	Araneidae	11.51	14.06
	Philodromidae	10.13	12.49
	Oxyopidae	10.41	4.60
	Theridiidae	2.67	1.10
	Gnaphosidae	0.55	0.55
	Lycosidae	0.37	0.32
Ants	Uloboridae	0.92	0.83
		9.97	11.21
	Tapinoma sp.	54.81	66.28
	Camponotus spp.	28.08	22.47
	Plagiolepis sp.	15.41	10.81
	Lasius sp.	1.12	0.23
	CreMATogaster sp.	0.45	0.05
Predatory Heteropteran	Pheidoles sp.	0.13	0.18
		33.98	25.72
Parasitoids	<i>Brachynotocoris ferreri</i>	65.96	54.40
	<i>Pseudoloxops coccineus</i>	15.63	14.62
	<i>Deraeocoris punctum</i>	16.04	19.60
	<i>Anthocoris nemoralis</i>	2.36	11.38
		40.14	56.17
	Scelionidae	49.98	46.09
Parasitoids	Encyrtidae	12.02	27.01
	Elasmidae	11.63	1.09
	Braconidae	7.04	1.33
	Ceraphronidae	0.72	0.79
	Chalcididae	0.25	0.07
	Megaspilidae	0.43	0.10
	Sphecidae	0.01	0.13
	Platygastridae	0.15	0.16
	Pteromalidae	1.18	1.62
	Diapriidae	0.09	0.01
	Mymaridae	0.83	1.66
	Eulophidae	1.51	0.63
	Eupelmidae	0.20	0.03
	Aphelinidae	4.40	5.65
	Bethylidae	0.09	0.05
	Trichogrammatidae	3.47	4.00
	Ichneumonidae	0.81	0.08
	Signiphoridae	5.20	9.51

4.3.4 Parasitoids

The best-fit model for parasitoids was the same as for spiders, and includes the effects of ground cover and adjacent natural vegetation ($AIC_c = 16163.60$; $R^2 = 0.59$; **Table 4.1**). The peak of abundance was 109 parasitoids/plot in ground cover plots and almost zero in bare soil plots (parameter a ; **Table 4.2**). The point of highest abundance and the width of the bell differed somewhat between years (parameters b and c respectively; **Table 4.2**).

Figure 4.1c summarises the effects of different types of natural vegetation on parasitoid abundance. The effect of herbaceous vegetation was negative for parasitoid abundance in bare soil plots and positive in ground cover plots (parameter $d.herb$; **Table 4.2**). Woody vegetation had an overall positive effect on abundance. There were almost no differences in the effects of woody vegetation patches on parasitoid abundance between bare soil or ground cover plots (parameter $d.lwp$; **Table 4.2**). However, the influence of small woody vegetation patches on abundance of ground cover plots was approximately one and a half times larger than that on bare soil plots (parameter $d.swp$; **Table 4.2**).

Model predictions showed a remarkable effect of patches that displayed a positive effect (all vegetation types except for herbaceous vegetation in bare soil plots, **Figure 4.1**) on the abundance of parasitoids (**Figure 4.2**). This effect was greater in bare soil plots.

At lower taxonomic levels, best-fit models for families Scelionidae, Elasmidae and Braconidae (**Table 4.3**), were similar to the one reported for the main group ($R^2 = 0.58$, $R^2 = 0.67$, $R^2 = 0.41$ respectively; **Table 4.4**). All effects were similar for Scelionidae and Elasmidae families, whereas for Braconidae there was a negative effect of herbaceous vegetation and small woody patches on ground cover plots (**Table 4.5**). No effects of ground cover or natural vegetation were found for Encyrtidae ($R^2 = 0.47$; **Table 4.4**).

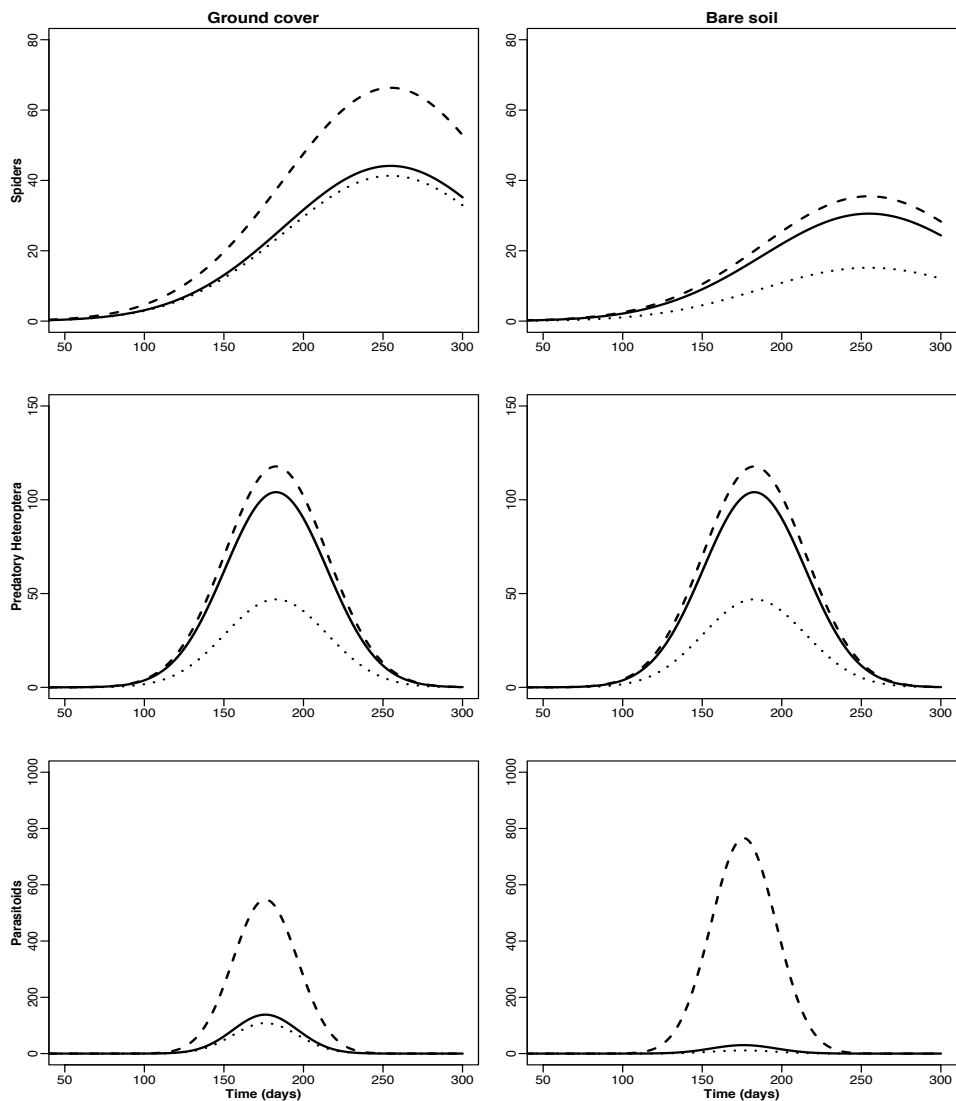


Figure 4.2 Model predictions for the abundance of the main natural enemy groups. Solid lines represent predicted abundance across time in the absence of adjacent natural vegetation. Upper dashed lines represent the estimated abundance in the most favourable conditions, i.e. under maximum density of vegetation patches that displayed a positive effect. Bottom dotted lines indicated model predictions in the least favourable conditions, i.e. under maximum density of vegetation patches that displayed a negative effect. Note that the specific conditions of positive and negative effects of vegetation patches may differ between ground cover and bare soil plots, as well as between the main groups of natural enemies (see **Figure 4.1**).

Table 4.4 Comparison of alternate models (using AIC_c) for the main natural enemy groups in olive groves.

		AIC _c															
		Spiders		Ants		Predatory Heteroptera			Parasitoids								
		Linyphiidae		Thomisidae		Salticidae		<i>Tapinoma sp.</i>	<i>Camponotus spp.</i>		<i>A. nemoralis punctum</i>	<i>D. coccineus</i>	<i>P. ferreri</i>	B. Scelionidae	Encyrtidae	Elasmidae	Braconidae
Basic model	No vegetation effect	1585.91	894.05	799.90	7903.88	1632.80	1614.63	2887.00	1640.48	3938.73	13979.79	14389.15	4871.21	2866.26			
	Interannual variability	1488.34	740.55	781.04	7498.36	1578.63	1209.03	2551.81	852.92	2893.26	13725.79	6691.76	1600.54	1620.59			
	Natural vegetation effect	1628.20	726.65	798.94	7150.50	1592.79	1600.82	2706.77	1636.13	3727.48	11925.11	8114.15	2541.13	2121.50			
	Interannual variability	1416.46	722.75	783.78	6561.38	1537.07	1179.41	2371.76	846.68	2692.20	11684.31	6619.88	1434.55	1608.82			
Ground cover model	No vegetation effect	1395.39	695.07	798.48	7639.41	1578.05	1615.78	2662.28	1633.95	3855.49	10775.48	8120.48	2774.14	2150.73			
	Interannual variability	1320.62	690.99	784.62	7233.93	1524.04	1355.03	2358.69	908.19	3450.89	10540.73	6828.79	1667.47	1637.98			
	Natural vegetation effect	1311.20	699.09	797.95	7147.63	1554.34	1601.35	2603.26	1636.14	3640.84	10120.79	8067.71	2541.17	2102.24			
	Interannual variability	1236.54	695.74	781.25	6742.37	1503.42	1340.75	2268.23	917.38	3145.79	9886.19	6776.26	1434.68	1589.62			
Ground cover x effect	Natural vegetation effect	1446.01	702.98	905.60	6549.78	1552.41	1548.56	2559.52	1623.31	3470.98	9981.19	8031.22	2497.92	2078.85			
	Interannual variability	1232.11	704.67	789.61	6144.58	1500.35	1288.12	2224.66	904.49	2977.34	9746.76	6739.72	1391.63	1566.39			
	R2 Best Model	0.42	0.40	0.32	0.15	0.43	0.38	0.38	0.38	0.84	0.73	0.58	0.47	0.67	0.41		
Parameters		11	6	8	12	12	9	12	9	9	12	6	12	12			

The best model (lowest AIC_c) is indicated in boldface type. The number of parameters and R² refer to the best model.

Table 4.5 Parameter estimates for the most parsimonious models of abundance of the lower taxonomic levels of the main natural enemy groups in olive groves.

	a			b			c			dherb	dlwv			dswv		
	Ground cover	Bare soil	2010	2010	2011	2010	2011	2010	2011		Ground cover	Bare soil	Ground cover	Bare soil	Ground cover	Bare soil
Linyphiidae	9	1		148		0.0324	0.0120			-653.5	-226.2	935.2	1108.1	403.18	4842.4	
Thomisidae	953118	402943		1048	1599	0.0057	0.0036									
Salticidae	928224	722708		1772		0.0032	0.0031			-2.74e ⁰⁷		9.92e ⁰⁷		-2.97e ⁰⁷		
<i>Tapinoma</i> sp.	9	13		121	1.01e ⁰⁶	0.0335	0.0031			1048.2	-4278.2	4479.9	1.35e ⁰⁴	-1.24e ⁰⁴	-593.3	
<i>Camponotus</i> spp.	19	5		228	337	0.0183	0.0081			-296.3	-1223.5	-1650	2086.8	1.31e ⁰⁴	9104.8	
<i>A. nemoralis</i>			5	15	150	134	0.0567	0.0530				516.2		-4164.1		
<i>D. punctum</i>	27	2.55e ¹³		135	113	0.0477	0.0384			-1405.8	810.7	-3010.4	3348.6	1e ⁰⁴	2.21e ⁰⁴	
<i>P. coccineus</i>			37	21	164	150	0.1146	0.0907				-567.7		6199.7		
<i>B. ferrei</i>			131	75	176	167	0.0661	0.0494				-1.30e ⁰⁴		-13216.2		
Scelionidae	51	1e ³²		178	172	0.0542	0.0501			1.02e ⁰⁴	-2426.6	4.22e ⁰⁶	2.61e ⁰⁴	1.24e ⁰⁵	9.47e ⁰⁴	
Encyrtidae	99	25		177	164	0.0418	0.0840									
Elasmidae	9	16		174	627	0.0688	0.0054			872.4	-1984.1	2.01e ⁰⁴	7239.4	1.52e ⁰⁴	3.52e ⁰⁴	
Braconidae	15	12		169	997	0.0451	0.0025			-12.5	-696.5	6440.5	553.3	-8139.7	2639.1	

4.4 Discussion

Two approaches have been traditionally adopted as an alternative to the use of insecticides in order to control insect pests in orchards: (1) implementation and maintenance of ground cover within the field; and (2) management of the adjacent natural vegetation. This study reveals that none of these approaches provide a unique response for all groups of arthropod natural enemies, and the combination of both can result in synergistic effects that are difficult to tell apart if analysed separately.

Overall, spiders, parasitoids, and the predatory Heteroptera *D. punctum* showed greater abundance in ground cover plots than in bare soil plots. The effects of the different types of adjacent natural vegetation and its interaction with ground cover were also dependent on the biology of the specific groups.

Spiders showed a strong preference for herbaceous habitats in previous studies (Sunderland and Samu 2000; Clough et al. 2005; Schmidt and Tschardtke 2005; Tschardtke et al. 2008; Pluess et al. 2010). When such habitats are found within the crop (i.e. ground cover), spiders can use trees, due to their proximity, as alternative resources to find food and shelter, particularly after senescence of the herbaceous vegetation in summer (Landis et al. 2000; Bianchi et al. 2006). For this reason ground cover increases spider abundance in the tree canopy. Patches of herbaceous vegetation around the crop will likewise be attractive for spiders, but will have the opposite effect for spiders found in the tree canopy, potentially promoting migration outside the grove (Schmidt and Tschardtke 2005). In the absence of ground cover, large woody vegetation may be more suitable for spiders than olive trees, possibly due to more prey variety and availability (Harwood et al. 2001), thus decreasing their abundance within the crop.

Models for ants were not particularly elucidating, as seen by the poor fit attained in the best-fit model. A very different behaviour of the two main genera (*Tapinoma* sp. and *Camponotus* spp.) might be obscuring the general group response. Other factors such as nest site availability, pressure from competing species and food resources could explain better their distribution (Buczowski and Bennett 2008).

Predatory Heteroptera were not affected by ground cover, except for *D. punctum*. Herbaceous vegetation and small woody patches found nearby and within the olive

grove did not exert an important effect on abundance. Three out of the four species (*P. coccineus*, *B. ferreri* and *D. punctum*) were mirids found at nymphal stage at the beginning of the season, which implies that they thrive in the tree canopy without any further interaction with the herbaceous layer. Large woody patches, on the contrary, had a negative effect on the abundance of predatory Heteroptera. Such a response might be related to intra-guild predation, since large woody patches increase the abundance of spiders and ants within the crop, which could prey on Heteroptera (Philpott and Armbrrecht 2006; Kobayashi et al. 2011). The absence of wings and the soft body of the nymphal stage of this group make it vulnerable to the attack by ants and spiders, supporting this hypothesis. The only species initially found at the adult stage was *A. nemoralis*, which has been reported as a species that overwinters in the surrounding natural habitat (Horton and Lewis 2000). For this species, the models predicted a positive effect, instead of negative effect, of large woody patches. Additionally, *D. punctum* reached higher abundances in ground cover plots than in bare soil plots. This could be related to a higher predation by *Tapinoma* sp. in bare soil plots, which was observed to appear at the same time in the olive canopy.

Ground cover had a large positive effect on parasitoids. The presence of adjacent natural vegetation also increased their abundance within the olive grove in accordance with the results found by Boccaccio and Petacchi (2009). Their dependence on herbaceous habitats, within or around the crop, as well as on woody vegetation, is much stronger than in other groups. In fact, in the absence of these structures (i.e. in bare soil plots with no adjacent natural vegetation) the predicted abundance for this group is zero. This could be because parasitoids, as specialist enemies, respond more strongly to landscape complexity at smaller scales (Chaplin-Kramer et al. 2011), highlighting the importance of ground cover to enhance their presence in orchards with a lower density of adjacent natural vegetation, and emphasizing the relevance of the analysis of the interaction between ecological infrastructures to understand the distribution of natural enemies within the crop.

Overall, ground cover seems to increase the abundance of most natural enemies and, therefore, this seems a promising option in order to enhance their populations (Danne et al. 2010; Silva et al. 2010). Small patches of woody vegetation interspersed within the crop play a minor role in sustaining populations of natural enemies, but contribute to

enhance the overall heterogeneity at the landscape scale (Clough et al. 2005). Large woody patches can help increase the populations of spiders and parasitoids, by creating alternative habitats that might provide a source of migrating individuals into the crop (Thomas et al. 1991; Bianchi et al. 2006). Yet in the absence of ground cover, such habitats can be more attractive for spiders, probably due to the scarcity of resources that ground cover provides, such as alternative preys (Costello and Daane 1998), which ultimately decrease their abundance within the crop. The presence of ground cover increases the positive effect that patches of herbaceous vegetation have on the abundance of parasitoids and reduces the negative effect on spiders reported for bare soil crops. This is a novel result that will help design habitat management strategies in olive groves, since the use of both complementary approaches produces a total effect that maximises the abundance of natural enemies within the crop.

Since the ultimate goal of habitat management strategies is to prevent insect pests, further research is needed to investigate whether the increase reported in the abundance of natural enemies will have an effect on the abundance of insect pests, as well as to elucidate the potential ecological mechanisms that might be involved (see Chaplin-Kramer et al. 2011).

4.5 References

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5

**Effect of non-crop vegetation types
on conservation biological control of
pests in olive groves**

Summary

Conservation biological control (CBC) is an environmentally sound potential alternative to the use of chemical insecticides. It involves modifications of the environment to promote natural enemy activity on pests. Despite many CBC studies increasing abundance of natural enemies, there are far fewer demonstrations of reduced pest density and very little work has been conducted in olive crops. In this study we investigated the effects of four forms of non-crop vegetation on the abundance of two important pests: the olive psyllid (*Euphyllura olivina*) and the olive moth (*Prays oleae*). Areas of herbaceous vegetation and areas of woody vegetation near olive crops, and smaller patches of woody vegetation within olive groves, decreased pest abundance in the crop. Inter-row ground covers that are known to increase the abundance of some predators and parasitoids had no effect on the pests, possibly as a result of lack of synchrony between pests and natural enemies, lack of specificity or intra-guild predation. This study identifies examples of the right types of diversity for use in conservation biological control in olive production systems.

Este capítulo reproduce íntegramente el siguiente artículo:

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5.1 Introduction

The use of synthetic pesticides for pest control in conventional agriculture is coming under closer scrutiny due to rising concerns about environmental and health problems (Meehan et al. 2011) including the recent ruling by the European Union to suspend the use of neonicotinoid insecticides (Stokstad 2013). Biological control has evolved in recent decades as a response to such concerns and one approach, conservation biological control, includes practices such as the modification of the environment to boost the impact of natural enemies of pests (Eilenberg et al. 2001). The modification of the environment can involve features on or close to farms (Boller et al. 2004), such as hedges, woodland patches, grasslands, wildflower strips, ruderal areas, conservation headlands and even stone heaps. The extent of spill-over of natural enemies between adjacent vegetation types can be large (Bowie et al. 1999). These various forms of modifications increase the diversity of vegetation and habitat structure, which in turn increases the availability of natural enemy resources such as nectar, pollen, alternative prey, and shelter (Altieri and Letourneau 1982; Landis et al. 2000).

The increase in natural enemy biodiversity that is often reported in studies with supplementary non-crop vegetation (Bianchi et al. 2006; Thies and Tscharntke 1999) can potentially increase ecosystem function in the form of top-down forces from the third to the second trophic level (Landis et al. 2000). Yet, the extent to which top-down forces are effectively activated by non-crop vegetation is variable and often not reported in papers that achieve effects purely at the third trophic level. Some studies have reported a decrease in herbivore density in the presence of ground cover vegetation (Aguilar-Fenollosa et al. 2011; Altieri and Schmidt 1986) or patches of natural vegetation in and around farms (Thies and Tscharntke 1999; Thomson and Hoffmann

2009), whilst others have found no effect (Bone et al. 2009; Danne et al. 2010). Lack of effect can be the result of intraguild predation (Polis et al. 1989; Straub et al. 2008), disruption of biological control by alternative prey presence (Koss and Snyder 2005) or asynchrony between herbivores and their natural enemies (Fagan et al. 2002; Perdakis et al. 2011). Additionally, there is the risk that pest species might be attracted by, and make use of non-crop vegetation, thus increasing – rather than decreasing – their abundance (Baggen and Gurr 1998; Gurr et al. 1998; Wratten and van Emden 1995). The foregoing factors underline the importance of identifying the right kinds of diversity for use in any conservation biological control program.

This study aimed to compare the relative benefits of four forms of vegetation diversity for use in olive grove conservation biological control (inter-row ground covers, areas of herbaceous vegetation and areas of woody vegetation near olive crops, and smaller patches of woody vegetation within olive groves) on the abundance of olive moth (*Prays oleae*), and olive psyllid (*Euphyllura olivina*).

There is a strong need for research on olive pests because world economic losses are estimated at € 800 million per year, with an additional cost of € 100 million year in agrochemical products (IOBC 2005). These figures do not include the potential environmental and health costs of insecticide use. Research on the potential for conservation biological control approaches to lessen reliance on insecticide use on olive pests is scarce (Herz et al. 2005). In the former chapter was detected that ground cover increased the abundance of spiders, Hymenopteran parasitoids and one species of predatory Heteroptera (*Deraeocris punctum*). If alternative forms of vegetation diversity can reduce pest abundance, the adoption of these by olive growers could alleviate the associated cost of conventional pest control, whilst potentially also improving other ecosystems services such as soil fertility, prevention of soil erosion (Cullen et al. 2008; Hartwig and Ammon 2002) and pollination (Tscheulin et al. 2011).

5.2 Material and methods

5.2.1 Study species

In this study we focused on the nymphs of *E. olivina* and the adults of the flower generation of *P. oleae*. The nymphs of *E. olivina* appear from mid April to the end of May and, during this period, are susceptible to the attack by natural enemies. The flower

generation of *P. oleae* is the most abundant of the three generations, and lays the eggs of the fruit generation. There is a strong correlation between the adults of the flower generation and the degree of olive fruit infestation (Ramos et al. 1989), and therefore it is assumed that controlling the population of the flower generation of *P. oleae* might ultimately reduce fruit infestation. Larvae of the flower generation of *P. oleae* appear at the same time as that of *E. olivina* nymphs. Other pests such as *Saissetia oleae* or *Bactrocera oleae*, that are potentially serious insects for the olive culture, were not included in this study because their attack was very low for the first in the study area. *B. oleae* used to appear from September to November, a period out of the target in this study. Several potential natural enemies of *E. olivina* and *P. oleae* were found in the experimental orchard. The most abundant were the spider families Thomisidae, Philodromidae, Araneidae, Salticidae, Linyphiidae and Oxyopidae; the parasitoids families Scelionidae, Encyrtidae, Elasmidae and Braconidae; the ant genus *Tapinoma* sp., *Camponotus* spp. and *Plagiolepis* sp.; the predatory Heteropteran species *Brachynotocoris ferreri*, *Pseudoloxops coccineus*, *Deraeocoris punctum* and *Anthocoris nemoralis*; and the green lacewing species *Chrysoperla carnea*.

5.2.2 Vegetation treatments

The study was conducted in an experimental olive grove (235 ha) located in southern Spain, near the city of Granada (37°17'N and 3°46'W). Four different forms of non-crop vegetation were investigated: inter-row ground covers, areas of herbaceous vegetation and areas of woody vegetation near olive crops, and smaller patches of woody vegetation within olive groves (**Figure 3.1**). Effects of the inter-row ground covers treatment were investigated by establishing 12 square-shaped plots each containing a grid of 7x7 olive trees and an area of 4900 m². Plots were separated by 150 m from each other. Half of the plots were treated with glyphosate and oxyflourfen in early spring 2010 and 2011 to remove weeds and provide a bare soil treatment. In the remaining plots, spontaneous herbaceous vegetation was allowed to grow in a 2.5 m wide strip between tree lines (**Figure 3.2a**). Climatic conditions were different in both years. Average annual precipitation was higher in 2010 (565.12 mm) than in 2011 (368.82 mm). In 2010 mean average temperature was lower (22.1°C) than in 2011 (24.5°C). Average maximum monthly temperature from April to June was 24.7°C in 2010 and 27.8°C in 2011. Ground cover was composed of herbaceous plants dominated by *Medicago minima*, *Anacyclus clavatus*, *Hordeum leporinum*, *Lolium rigidum*, and

Bromus madritensis. The area beside the groundcover strips were treated with the same herbicides used for the bare soil treatment. No insecticides were used in the grove for two years before the beginning of the experiment onwards. Other treatments were naturally occurring vegetation patches.

Herbaceous vegetation was adjacent to some of the olive areas and dominated by *Anchusa* sp., *Anacyclus clavatus* and *Echium plantagineum* (**Figure 3.2b**). Likewise, large woody patches were present beside some areas of olives as relatively extensive areas, partly in ravines, and comprised predominantly of *Phyllirea angustifolia* and *Quercus rotundifolia* (**Figure 3.2c**). Finally, small woody patches were comprised of shrubby vegetation patches occupying no more than a few square meters and located within the olive area, usually at hilltops, in areas of difficult access to machinery (**Figure 3.2d**). This community consisted mainly of *Genista hirsuta*, *Cistus albidus*, *Cistus clusii*, and *Rosmarinus officinalis*.

Arthropod samples were collected every ten days, weather allowing, from late March to early July in 2010 and from early April to early July in 2011 giving 12 sampling dates in 2010 and nine dates in 2011. Sampling employed a modified vacuum device, CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, Florida, USA), which was used for two minutes per tree. On each date 16 olive trees (a grid of 4x4) were randomly selected for sampling (**Figure 3.3b**). Arthropods were stored on ice for transportation to the laboratory, where they were identified and counted.

To incorporate the effect of each type of vegetation in models of *E. olivina* and *P. oleae* abundance (see below), we digitized all patches of non-crop vegetation using aerial photographs, and a 1x1 m resolution grid was superimposed upon the resulting vector maps. A bivariate Gaussian kernel density function (Diggle 1985) was computed from the 1x1 m grid and a value was calculated for each plot in order to obtain a distance-weighted measure of the influence of each vegetation type on that plot. As we hypothesize that pest densities are going to be mediated by trophic interactions with their potential natural enemies, a standard deviation of 120 m was chosen for the Gaussian kernel density function, as Miliczky and Horton (2005) reported this as the maximum distance of dispersal of some groups of natural enemies in orchards. This measure also allowed incorporating the influence of vegetation at distances further than

120 m by assigning progressively lower weights, by means of the Gaussian density function, as we moved away from the plot. These analyses were performed with the R package 'spatstat' (Baddeley and Turner 2005).

5.2.3 Data modelling

A gaussian function was used to describe the predicted abundance of the pests in response to time, since these insects typically show an increase in abundance during spring, reaching a maximum and declining afterwards. The gaussian curve is a characteristic symmetric "bell curve" shape defined by three parameters: a , b and c . Parameter a is the height of the curve's peak; in our case, the maximum abundance that a certain pest could reach. The point in time when the highest abundance is reached is represented by parameter b , which is days since the first of January, and represents the mean of the gaussian curve. Parameter c represents the standard deviation and controls the width of the "bell". The simplest model is represented by the equation:

$$Abundance = a \cdot \exp\left(-\left(\frac{(x-b)^2}{2c^2}\right)\right) \quad \text{Equation 5.1}$$

where X is time, measured in days.

We added to the function a set of new parameters ($d.herb$, $d.lwp$, $d.swp$) that reflect the effect of herbaceous, large and small woody vegetation density on pest abundance. These account for the effect of each vegetation type on the estimated curve's peak (parameter a). A positive or negative effect means an increase or a decrease of pest abundance, respectively. The basic gaussian function was modified to account for differences in the estimated parameters across plot treatments (ground cover and bare soil; parameter a and d) and years (2010, 2011; parameters a , b , c and d). We used likelihood methods and model selection as an alternative to traditional hypothesis testing (Johnson and Omland 2004; Canham and Uriarte 2006), for data analysis. Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the abundance measured in the field, given a suite of alternative models. Overall, we tested 60 models, 20 more than in the former chapter due to we allow the parameter d to vary between years. The most complex

model, taking into account the effects of ground cover, natural vegetation, the interaction between these two, and inter-annual variability, can be expressed as:

$$Abundance = (a_{ij} + \gamma_{ij}) \cdot \exp\left(-\left(\frac{(x - b_i)^2}{2c_i^2}\right)\right) \quad \text{Equation 5.2}$$

where g_{ij} represents the effect of natural vegetation patches on the maximum abundance of pests in each treatment (j) and year (i), which results from multiplying parameters $d.herb_{ij}$, $d.lwp_{ij}$ and $d.swp_{ij}$, estimated separately for bare soil and ground cover each year, by the observed values of herbaceous ($Xherb$), large ($Xlwp$) and small woody patches ($Xswp$) density, respectively, according to the following expression:

$$\gamma_{ij} = (d.herb_{ij} \cdot Xherb + d.lwp_{ij} \cdot Xlwp + d.swp_{ij} \cdot Xswp) \quad \text{Equation 5.3}$$

We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e. the parameters that maximize the log-likelihood) given our observed data (Goffe et al. 1994). We used a Poisson error structure for all response variables. Alternative models were compared using the Akaike Information Criterion (AIC_c) corrected for small sample size (Burnham and Anderson 2002). Models with a difference in $AIC_c > 2$ indicate that the worst model has virtually no support and can be omitted from further consideration. We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). The R^2 of the model fit ($1 - SSE/SST$, sum of squares error (SSE) sum of squares total (SST)) of observed versus predicted was used as a measure of goodness-of-fit. All analyses were performed using the 'likelihood' package (Murphy 2012) written for the R environment (R Development Core Team 2012).

Based on best model predictions, we calculated the proportional change in pest abundance under the influence of a single vegetation type (PCA_{VT}) as follows:

$$PCA_{VT} = \Delta A_{VT} / \text{Maximum abundance} \quad \text{Equation 5.4}$$

where ΔA_{VT} is the difference between the predicted abundance in the presence of ground cover or maximum vegetation density for a particular vegetation type and the predicted abundance in the absence of any ecological infrastructure. PCA_{VT} ranks from 1 to -1, reflecting the proportional increase (positive values) or decrease (negative values) of pest abundance under the influence of a particular vegetation type.

5.3 Results

A total of 7,530 insects were trapped during the study. Of these 4,940 were adults of *P. oleae* and 2,590 were nymphs of *E. olivina*. For both of these major pests, the best model included the effect of vegetation and inter-annual variability in the parameters *a*, *b*, *c* and *d* (*E. olivina*: $R^2 = 0.60$; *P. oleae*: $R^2 = 0.95$; **Table 5.1**). Ground cover did not have any effect on the abundance of pest species and consequently we did not calculate the proportional change in abundance for ground cover versus bare soil.

Both species displayed differences in abundance

between years. *Euphyllura olivina* displayed a two-fold lower abundance in 2010 (45 individuals/plot) than in 2011 (94 individuals/plot) (**Table 5.2**). For *P. oleae* the opposite temporal trend was apparent with 213 individuals/plot in 2010 but only 90 individuals/plot the following year (**Table 5.2**).

Table 5.1 Comparison of alternative models using AICc.

			AICc	
			<i>E. olivina</i>	<i>P. oleae</i>
Basic model	No Vegetation effect	General response	2497.99	2270.00
		Interannual variability	1829.50	879.19
		General response	2310.68	2248.13
	Natural vegetation effect	Interannual variability	1693.24	862.91
		General response	2437.80	2266.97
		General response	2239.37	2247.25
Cover crop model	No Vegetation effect	General response	2437.80	2266.97
		Interannual variability	2050.68	1639.93
		General response	2239.37	2247.25
	Natural vegetation effect	Interannual variability	2237.08	2121.30
		General response	2263.38	2255.42
		General response	2263.38	2255.42
Natural vegetation effect x cover crop	Interannual variability	1852.42	1621.31	
	R ² Best Model	0.60	0.95	
	Number of Parameters Best Model	12	12	

The best model (lowest AIC_c) is indicated in boldface type. The number of parameters and R² refer to the best model. For brevity, we have presented in **table 5.1** only the most parsimonious (i.e. lowest AIC_c) of all possible models that include inter-annual variability with one, two or three parameters varying between years.

The effect of vegetation varied among pests and years (**Table 5.2**). Proportional change in abundance (PCA_{VT}) allowed quantifying the relative effect of each vegetation type on pest abundance, whether positive or negative (**Figure 5.1**). Herbaceous vegetation had a

Table 5.2 Parameter estimates and two-unit support intervals (in brackets) for the most parsimonious models of abundance of the pests tested in this study.

	<i>E. olivina</i>	<i>P. oleae</i>
a		
2010	45 [48; 53]	213 [209; 220]
2011	99 [96; 102]	90 [86; 95]
b		
2010	129	169
2011	120	162
c		
2010	0.102 [0.098; 0.104]	0.152 [0.151; 0.154]
2011	0.090 [0.087; 0.093]	0.178 [0.172; 0.184]
d.herb		
2010	-1474.32 [-1956.04; -871.91]	-6097.19 [-7429.27; -4388.74]
2011	-2276.73 [-2972.59; -1574.81]	-707.05 [-1869.73; -602.28]
d.lwp		
2010	-1034.20 [-2683.31; -909.83]	-14650.07 [-18665.02; -9521.84]
2011	5164.31 [2588.72; 7543.65]	-3797.50 [-6992.69; 348.83]
d.swp		
2010	-11190.67 [-5847.34; 15541.83]	-5691.26 [-18370.29; 7631.83]
2011	-86071.63 [-79770.35; 92788.34]	18960.74 [8730.12; 29823.10]

Parameter *a* is the maximum abundance of the pest in each year (2010, 2011); *b* and *c* represent the mean and standard deviation of the Gaussian curve in different years. The parameters *d.herb*, *d.lwp* and *d.swp* represent the effect of natural vegetation on the maximum abundance of the pests in each year.

2010 and 2011, respectively, but had no effect in 2010 and a positive effect in 2011 with *E. olivina* increasing in abundance by 13% (**Figure 5.1**).

negative effect on the abundance of both pests in both years (**Figure 5.1**).

For *P. oleae* this effect was associated to a reduction in abundance of ca. 20% in 2010, but the reduction was much smaller in 2011 (**Figure 5.1**).

For *E. olivina* there was a reduction in abundance of ca. 20% in both years (**Figure 5.1**).

Small and large woody vegetation was associated to opposing responses for the two pests. For *E. olivina*, the influence of small woody vegetation was associated to a

reduction the population by 16% and 59% in 2010 and 2011, respectively (**Figure 5.1**).

For *P. oleae* there was a negligible effect in 2010 and an estimated increase of ca. 12% in 2011 (**Figure 5.1**).

Large woody vegetation was associated to a reduction of *P. oleae* by 19% and 11% in

2010 and 2011, respectively, but had no effect in 2010 and a positive effect in 2011 with *E. olivina* increasing in abundance by 13% (**Figure 5.1**).

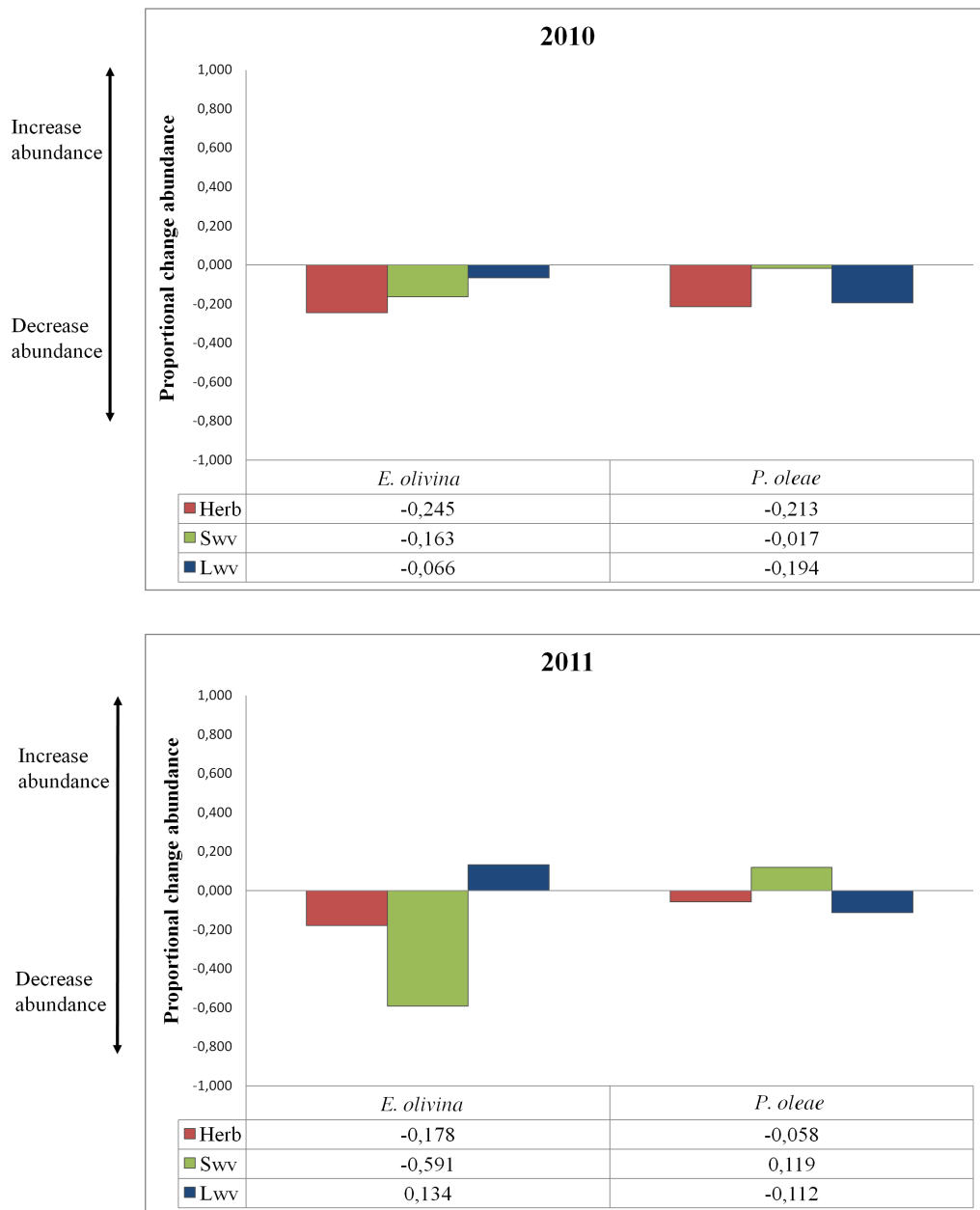


Figure 5.1 Proportional change abundance of the pests under the influence of different ecological infrastructures for both years of the study.

5.4 Discussion

Non-crop vegetation can have the effect of suppressing pest populations by increasing the abundance of different groups of natural enemies (Thies and Tschardtke 1999; Landis et al. 2000; Boller et al. 2004; Bianchi et al. 2006) provided that the right types of vegetation are identified and promoted for use. In this study herbaceous and woody

vegetation within or adjacent to olive groves offered scope to reduce pest abundance through an indirect effect rule by the presence of natural enemies. Specifically, herbaceous vegetation was associated with a consistent reduction of the abundance of both pests though this effect was slight for *P. oleae* in 2011 when this pest was relatively rare. Small woody areas within the olive crop were associated with a reduction of *E. olivina* in both years but especially in 2011 when this pest was relatively common, giving a reduction of nearly 60%. For *P. oleae*, small woody areas gave a significant reduction in 2010 when this pest was relatively common but a modest increase in the following year when its density was relatively low. In contrast, the influence of large woody vegetation patches led to decreased pest abundance except for *E. olivina* in 2011 when this pest was relatively common. The consistent effect found in this study (large woody vegetation on the abundance *P. oleae* and small woody vegetation on the abundance of *E. olivina*) could be due to large uncultivated areas being better source of natural enemies than small areas (Tschardt et al. 2008) but, small areas distributed within the crop may facilitate natural enemies to move quickly into the crop (Bianchi et al. 2006). As *P. oleae* appears later than *E. olivina* this could explain why small woody vegetation affects more consistently to *E. olivina* and large woody vegetation to *P. oleae*.

Reductions in pest numbers are likely to be associated with enhanced densities of predatory Heteroptera in olive plots as a response to herbaceous and small woody vegetation (Chapter 4) as these pests, especially *E. olivina*, are highly specific for olive and changes to their numbers would have nothing to do with emigration. Members of this taxon, such as *Anthocoris nemoralis* or *Deraeocoris punctum*, have been described as predators of both *E. olivina* and *P. oleae* (Kidd et al. 1999; Morris et al. 1999a; Scutareanu et al. 1999; Agustí et al. 2003). The variability observed between years in the proportional change of abundance of the two pest species might suggest an important role of climatic conditions in modulating pest responses to their environment. Changes in temperature and humidity could alter the phenology of pests and natural enemies and, therefore, influence insect population growth rate (Wolda 1988; Logan et al. 2006), which might ultimately change the effectiveness of natural enemies in controlling pest abundance from one year to the next.

There was no effect of inter-row ground covers and this is consistent with the results reported by Albedis et al. (2004) and Rodriguez et al. (2009). Notably, inter-row ground covers were found to increase the abundance of different groups of natural enemies including spiders, parasitoids and ants in an earlier study of this system (Chapter 4) but the present results indicate a lack of top down effects on *P. oleae* and *E. olivina*. This could reflect a lack of synchrony between these herbivore species and the natural enemies that exhibited a response to ground cover vegetation. Studies in other systems have indicated the significance of synchrony for pest suppression (Fagan et al. 2002; Perdakis et al. 2011). This means an increase in the abundance of natural enemies promoted by ground cover occurs at a time of the year when pest abundance is low. This could be the case for spiders, which were enhanced by ground cover (Chapter 4) but reach their maximum abundance by mid August. This contrasts with the nymphs of *E. olivina* and the eggs and larvae of *P. oleae* that reach their maximum densities much earlier, in April or May. Thus, spiders are responding to prey availability rather than suppressing population increase. Alternatively, the species of natural enemies favoured by ground cover might not be those that utilise *E. olivina* and *P. oleae* as prey. Parasitoids clearly fall within this category, since most of those reported to be enhanced by ground cover (Chapter 4) are not specific for the study pest species. Parasitoids of *E. olivina* and *P. oleae* mainly belong to families Encyrtidae and Elamidae, which represent together less than 30% of the abundance of those reported from this study system. In fact, 50% of the parasitoids belonged to the hymenopteran family Scelionidae, which mostly attack the eggs of spiders (Fitton et al. 1987) and chrysopids in olive groves (Campos 1986). This intraguild predation would weaken top-down forces in olive groves. Related to this effect, the increase in abundance of ants reported in the former chapter of this document might have a detrimental effect on other natural enemies in olive groves (Morris et al. 1999b; Pereira et al. 2004). In summary, even though ground cover enhanced the populations of some groups of natural enemies, this did not lead to reduce pest abundance so is not an optimal form of vegetation for use in olive conservation biological control.

This study has indicated the relative suitability of various types of non-crop vegetation in conservation biological control of *E. olivina* and *P. oleae* and provides an example of how such studies can help growers achieve the sometimes difficult task of balancing the practicalities of conserving appropriate forms of vegetation in ways that cause little or

no disruption to normal agronomic practices (Gurr et al. 2005). *Prays oleae* is currently the principal insect pest in olive groves in the Mediterranean Europe so it needs to be the primary target of management. Against this pest, herbaceous vegetation and large woody vegetation adjacent to olive crops provided the most consistent level of suppression. Small woody vegetation within olive groves appears less suitable as it gave modest reductions or increases in *P. oleae* densities. In areas where *E. olivina* is more likely to be the primary pest, small woody vegetation within olive groves offers more value, especially since its presence led to major reductions in the study year during which it was more common. Inter-row ground covers are shown to be unsuitable because, though these promote various natural enemy taxa, they do not provide suppression of either of the major pests. A longer-term study would be important to validate these tentative recommendations and identify precisely the underlying ecological process that can influence the success of olive pest conservation biological control.

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6



Single best species or natural enemy assemblages? A correlational approach to investigating ecosystem function

Summary

Though biodiversity can have an effect on biological control of pests, there is debate about whether a single species or a more complex assemblage of natural enemies will exert better control of the pest population. We explore the relationship between numbers of different taxa of natural enemies in an olive grove to identify cases of significant positive and negative correlations between enemy taxa. Integrating herbivore data identified enemy taxa and assemblages that were associated with low numbers of olive pests. Overall, single species such as *Anthocoris nemoralis*, or relatively simple predator assemblages, such as that formed by the spider families Araneidae and Liniphiidae, and the green lacewing *Chrysoperla carnea*, were associated with better biological control than complex assemblages, where intra-guild predation and other trophic interactions might hamper the effectiveness of enemies. For a Lepidopteran pest with a complex life cycle, the single best predator taxon was markedly poorer at suppression than the most effective assemblage. In contrast, a Hemiptera pest with a simple life cycle was controlled nearly as well by the single best predator taxon as by the most effective assemblage. Statistical approaches offer good scope to identify optimal aspects of biodiversity to maximise ecosystem services such as biological control.

Este capítulo reproduce íntegramente el siguiente artículo:

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6.1 Introduction

In agricultural systems, biodiversity can have a profound effect on ecosystem function and offers potential benefits in the form of ecosystem services such as biological control of pests (Letourneau et al. 2009; Gurr et al. 2012). Nevertheless, knowledge about the nature of the interactions between natural enemies is needed to optimally manipulate components of biodiversity and, thereby, maximise the delivery of ecosystem services (Cardinale et al. 2003; Wilby et al. 2005). From a “biodiversity-ecosystem function” assemblages of multiple natural enemies can reduce the density of agricultural pests (Symondson et al. 2002; Cardinale et al. 2003; Cardinale et al. 2006), but there is debate about whether a single species or a simple natural enemy assemblage will exert better control of a pest population than will more complex assemblages (Hassel and May 1986; Denoth et al. 2002). Predators can interact antagonistically and disrupt biological control or positively with the opposite outcome for this ecosystem service (Rosenheim et al. 1995; Hodge 1999; Finke and Denno 2004).

Straub et al. (2008) proposed three potential outcomes by which increased species richness might impact pest control: a reduction of pest density, a neutral effect, or a disruption of biological control. The first is an outcome of a niche complementarity whereby a single pest species can provide multiple types of prey resource that are fully exploited only by more than one enemy species. Two mechanisms can lead to this process, resource partitioning and facilitation (Hooper et al. 2005). Alternatively, a neutral effect on pest density may arise if multiple enemy species are functionally redundant so all exploit the same prey resource in the same microhabitat at the same time. Increasing the number of species with the same function leads to interspecific competition (Ives et al. 2006). Finally, intra-guild predation occurs when a top predator

(intra-guild predator) consumes an intermediate predator (intra-guild prey), with which it competes for a common prey resource (the pest) (Polis et al. 1989; Polis and Holt 1992). So, for conservation biological control practitioners, determining when multiple predator species provide better pest suppression than single species is a key step towards developing ecologically-informed pest management (Ehler 1990; Straub et al. 2008).

This study investigated the relationships amongst predator natural enemies and two pest species in olive groves. The study is built on research on the effects of habitat management (ground cover and different types of vegetation adjacent to the crop) on the abundance of different groups of natural enemies (Chapter 4) and two important pests in olive groves: the olive moth (*Prays oleae*) and the olive psyllid (*Euphyllura olivina*) (Chapter 5). The results of those studies revealed that: 1) patches of adjacent natural vegetation increased the abundance of some groups of natural enemies (Chapter 4) and decreased the abundance of pests (Chapter 5); and 2) ground cover increased the abundance of most natural enemies (Chapter 4), but had no effect on pests (Chapter 5). Such results suggest that potential interactions amongst natural enemies might obscure the response of pest abundance to different habitat management strategies. Therefore, this study aimed to analyse correlations between natural enemy assemblages and pest abundances in order to test for the action of the mechanisms described by Straub et al. (2008) and thereby identify the natural enemy taxa or assemblages most strongly associated with reduce pest densities in olive groves.

Specific goals of the research were: 1) to explore correlations between the numbers of natural enemy taxa; 2) to investigate the relationship between assemblages of natural enemies and key pest species using unconstrained ordination; and 3) to identify particular assemblages of natural enemies that best correlate with low pest abundance. Following Wilby et al. (2005), we hypothesised that prey with a more complex life cycle, such as the holometabolous *P. oleae*, would be better suppressed by a more diverse natural enemy assemblage than would herbivores with a simpler life cycle, such as the hemimetabolous *E. olivina*. Because our analyses are based on correlations between variables, causality cannot be inferred. Yet our study provides a novel statistical approach for exploring the relationship between biodiversity and ecosystem function. In the particular case of biological pest suppression, this work provides

empirical evidence to untangle the ecological processes underlying positive and negative interactions between natural enemies and their prey and, thereby, constitutes a framework for guiding conservation biological control.

6.2 Material and methods

6.2.1 Study area and experimental design

The study was conducted in an olive grove of 235 ha located in southern Spain, near the city of Granada (37°17'N and 3°46'W), during 2010 and 2011. The grove comprised two adjacent zones separated from each other by a creek occupied by natural vegetation (**Figure 3.1**). A further description of the study area can be found chapter 2, 4 and 5.

The basic experimental unit in our study was the plot. There were a total of twelve equidistant plots, which were sampled on different dates (**Figure 3.3a**). Each plot had a square shape comprising 7x7 olive trees and an area of 4900 m², as olive trees were 10 m apart from all other adjacent olive trees (**Figure 3.3b**). Within each plot, a square of 4x4 olive trees was randomly selected at each date, corresponding to an area of 1600 m² (**Figure 3.3b**). Samples were collected every ten days, weather allowing, from early April to early July in 2010 and in 2011, which is the period when the two main pests analysed in this study were found in the orchard. Overall there were ten sampling dates in 2010 and nine sampling dates in 2011. A modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, Florida, USA) was used to trap the arthropods in the canopy of each of the 16 olive trees (two minutes per tree).

6.2.2 Arthropod taxa

The most common predators known to eat the two studied pest species were considered in our study (Morris et al. 1999a). Of them five were spider families: Thomisidae, Philodromidae, Araneae, Linyphiidae, Salticidae; three were ant genera: *Camponotus*, *Tapinoma* and *Plagiolepis*; four were predatory Heteropteran species: *Deraeocoris punctum*, *Anthocoris nemoralis*, *Brachynotocoris ferreri* and *Pseudoloxops coccineus*; and one was a green lacewing species: *Chrysoperla carnea*.

Two pest species typically of olives were considered in this study: the flower generation of the olive moth (*Prays oleae*) and the olive psyllid (*Euphyllura olivina*) (**Figure 1.2 b** and **d** respectively). The flower generation of *P. oleae* is the most abundant of the three

generations, and lays the eggs of the fruit generation. There is a strong correlation between the numbers of adults of the flower generation and the degree of olive fruit infestation (Ramos et al. 1989), and therefore it is assumed that controlling the population of the flower generation of *P. oleae* might ultimately reduce fruit infestation. Eggs and larvae of the flower generation of *P. oleae* appear at the same time as that of *E. olivina* nymphs, but are not efficiently sampled by the vacuum method used in the present study.

6.2.3 Data analysis

To analyse the data and avoid temporal autocorrelation of samples, we pooled together all samples taken each year. Thus for each plot we obtained a representative measure of the overall abundance of each natural enemy and pest species for 2010 and 2011, which were treated in further analyses as independent samples.

Pearson's correlations were initially obtained to look at the relationships between the abundance of pairs of natural enemies. Negative correlations would indicate intra-guild predation or resource competition, whereas positive correlations would indicate niche complementarity.

Non-metric multidimensional scaling (NMDS) was used to investigate the overall pattern of species composition in the predator assemblages, and group species that could respond similarly to environmental conditions, habitat structures and resource availability. Data were square-root transformed and then subjected to Wisconsin double standardization (Legendre and Gallagher 2001). We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix among plots. To explore associations between particular predator species or assemblages and pest species, we generated smooth surfaces for the two pest abundances on the NMDS ordination diagram. Smooth surfaces are the result of fitting thin plate splines using general additive models and interpolating the fitted values on the NMDS plot (Oksanen et al. 2012).

Mantel test of matrix correspondence was used to determine whether similarities in predator assemblages were correlated with similarities in pest abundance for each pest species. The standardised form of the Mantel test was used, which computes the Pearson's correlation coefficient. The statistical significance of each correlation was

determined by a Monte Carlo test with 999 permutations. Mantel tests for the best possible subsets of predator abundances (Clarke and Ainsworth 1993) were also run on distances matrices to select the combination of predatory species that most contributed to explaining the variability in pest abundance.

All the analyses were performed with the R software (R Development Core Team 2012), including the 'vegan' package (Oksanen et al. 2012).

6.3 Results

We collected a total of 26,490 arthropods; 14,484 in 2010 and 12,006 in 2011 (**Figure 6.1**). Most of the significant correlations between predator taxa were positive (**Table 6.1**). One exception to this was *A. nemoralis*, which displayed significant negative correlations with *Plagioleipsis* ($r=-0.489$; $p=0.015$; **Table 6.1**), *Camponotus* ($r=-0.584$; $p=0.003$; **Table 6.1**), *B. ferreri* ($r=-0.622$; $p=0.001$; **Table 6.1**) and *P. coccineus* ($r=-0.404$; $p=0.05$; **Table 6.1**). These four arthropods were associated with a high abundance of *P. oleae* (**Figure 6.1**). Also the ant *Tapinoma* displayed negative correlation with the vast majority of the other predators, but only significant with *D. punctum* ($r=-0.426$; $p=0.038$; **Table 6.1**).

A. nemoralis and *Tapinoma* showed a significant positive relation ($r=0.438$; $p=0.035$; **Table 6.1**) and appeared associated to a high abundance of *E. olivina* and low abundance of *P. oleae* (**Figure 6.2**). Also associated to a low abundance of *P. oleae*, we found an assemblage of predators conformed by the spider families Araneidae, Linyphiidae and the green lacewing *C. carnea* (**Figure 6.2**). The components of this assemblage were also positively and significantly correlated to each other (**Table 6.1**).

There was a significant correlation between predator assemblages and *P. oleae* ($r=0.323$; $p=0.001$) and *E. olivina* ($r=0.542$; $p=0.001$), as revealed by Mantel tests. The selection of subsets of predator species that had the best correlations with the two pest species indicated that a highest proportion of the variation in their abundance could be explained by three and five taxa, respectively (**Table 6.2**). The predators *B. ferreri*, *P. coccineus* and *A. nemoralis* explained 49% of the variation in *P. oleae*, whereas Thomisidae, Salticidae, *Tapinoma*, *P. coccineus* and *A. nemoralis* explained 53% of the variation in *E. olivina* (**Table 6.2**).

Table 6.1 Pearson's correlation matrix between predator taxa

	Thomisidae	Phlodiromidae	Araneidae	Linyphiidae	Salticidae	Plagiolēpis	Camponotus	Tapinoma	<i>B. ferreri</i>	<i>P. coccineus</i>	<i>D. punctum</i>	<i>A. nemoralis</i>	<i>C. carnea</i>
Thomisidae	1.000												
Phlodiromidae	0.028	1.000											
Araneae	0.254	0.411**	1.000										
Linyphiidae	0.198	0.483**	0.722***	1.000									
Salticidae	0.070	0.290	0.034	0.059	1.000								
Plagiolēpis	0.118	-0.027	-0.215	-0.042	0.039	1.000							
Camponotus	0.551**	0.206	0.142	0.030	0.107	0.283	1.000						
Tapinoma	-0.252	-0.098	-0.160	-0.114	0.290	-0.220	-0.353	1.000					
<i>B. ferreri</i>	0.395	-0.082	-0.185	-0.138	-0.011	0.029	0.443*	-0.152	1.000				
<i>P. coccineus</i>	0.357	0.141	0.110	0.017	-0.174	0.494**	0.288	-0.373	0.357	1.000			
<i>D. punctum</i>	0.589**	0.263	0.623**	0.706***	-0.008	0.223	0.433*	-0.426*	0.204	0.460*	1.000		
<i>A. nemoralis</i>	-0.200	0.105	0.156	0.054	0.205	-0.489*	-0.584**	0.438*	-0.622**	-0.404*	-0.258	1.000	
<i>C. carnea</i>	0.514**	0.260	0.722***	0.589**	-0.139	-0.211	0.234	-0.278	-0.059	0.077	0.677***	0.191	1.000

Significant correlations in bold. ***p ≤ 0.001; **p ≤ 0.01; *p ≤ 0.05.

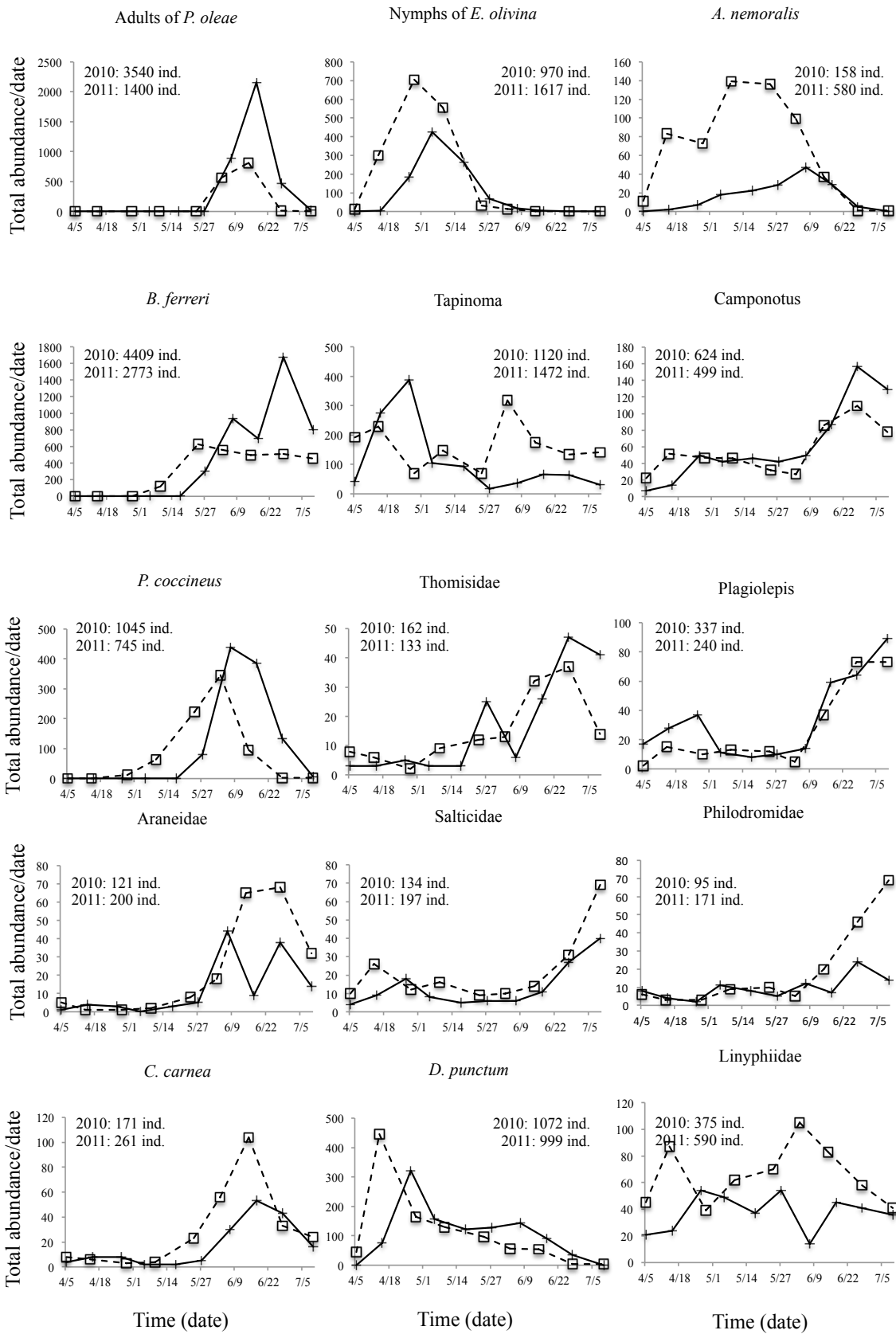


Figure 6.1 Temporal distribution of the arthropods tested in this study. Solid lines and cross represent the year 2010. Dashed lines and squares represent the year 2011. As legend in every plot the total sum of the abundance for every year.

For *P. oleae*, the single best taxon (*A. nemoralis*) gave markedly weaker pest suppression than did the best-performing assemblage. In contrast, the single best taxon for *E. olivina* suppression (*Tapinoma*) gave only marginally weaker suppression than did the incrementally more complex and the best-performing assemblage (**Table 6.2**).

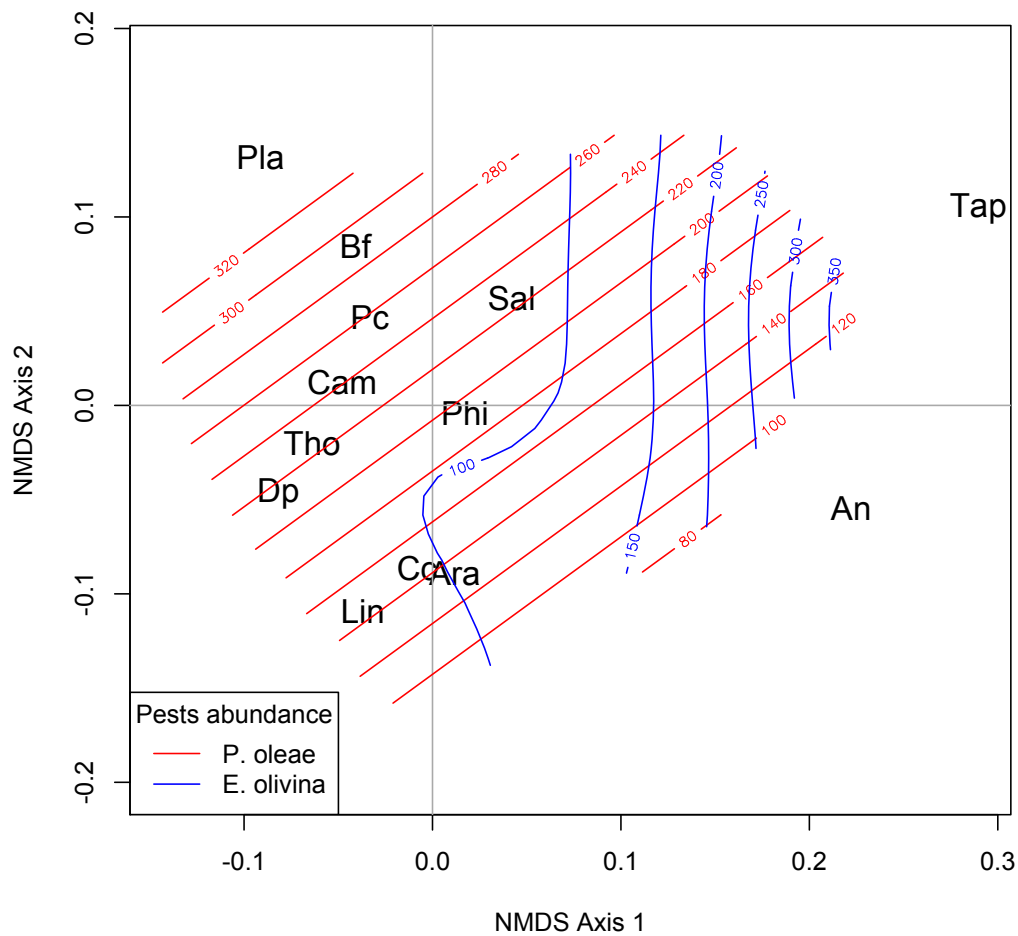


Figure 6.2 Non metric multidimensional scaling (NIMDS) of total predator abundance in 12 plots sampled in 2010 and 2011. The ordination axes have been related with the two main pest species abundance by means of generalized additive models. Red lines represent the abundance of *P. oleae*. Blue lines represent the abundance of *E. olivina*. Tho: Thomisidae; Phi: Philodromidae; Ara: Araneae; Lin: Linyphiidae; Sal: Salticidae; Cam: Camponotus; Tap: Tapinoma; Pla: Plagiolepis; Dp: *D. punctum*; An: *A. nemoralis*; Bf: *B. ferreri*; Pc: *P. coccineus*; Cc: *C. carnea*.

Table 6.2 Correlation of predator subsets with pest species.

<i>P. oleae</i>		<i>E. olivina</i>	
An	0.373	Tap	0.508
BfAn	0.457	Tap Pc	0.450
BfPc An	0.490	Tap Pc An	0.478
Ara BfPc An	0.459	Tho Tap Pc An	0.508
Cam Tap BfPc An	0.430	Tho Sal Tap Pc An	0.530
Ara Cam Tap BfPc An	0.418	Tho Sal Tap Pc Dp An	0.510
Ara Pla Cam Tap BfPc An	0.398	Tho Sal Tap BfPc Dp An	0.495
Tho Ara Pla Cam Tap BfPc An	0.366	Tho Sal Pla Tap BfPc Dp An	0.482
Tho Phi Ara Pla Cam Tap BfPc An	0.337	Tho Lin Sal Pla Cam Tap Pc Dp An	0.470
Tho Phi Ara Pla Cam Tap BfPc An Cc	0.312	Tho Lin Sal Pla Cam Tap BfPc Dp An	0.455
Tho Phi Ara Sal Pla Cam Tap BfPc An Cc	0.287	Tho Lin Sal Pla Cam Tap BfPc Dp An Cc	0.440
Tho Phi Ara Sal Pla Cam Tap BfPc Dp An Cc	0.265	Tho Phi Lin Sal Pla Cam Tap BfPc Dp An Cc	0.415
Tho Phi Ara Lin Sal Pla Cam Tap BfPc Dp An Cc	0.239	Tho Phi Ara Lin Sal Pla Cam Tap BfPc Dp An Cc	0.379

In bold best subset. Tho: Thomisidae; Phi: Philodromidae; Ara: Araneae; Lin: Linyphiidae; Sal: Salticidae; Cam: Camponotus; Tap: Tapinoma; Pla: Plagiolepis; Dp: *D. punctum*; An: *A. nemoralis*; Bf: *B. ferreri*; Pc: *P. coccineus*; Cc: *C. carnea*.

6.4 Discussion

Untangling the relationships amongst predator species in the arthropod assemblages is not straightforward as there are many paths, direct or indirect, that may be involved. Results revealed that certain predator assemblages are significantly correlated with the two pest species, but there are positive and negative interactions in the natural enemies assemblages that might be interfering with the response of pests to predators. We found that the prey species with the more complex life cycle, *P. oleae*, was best suppressed by a richer assemblage of three enemy taxa whereas the prey with a simpler life cycle, *E. olivina*, was best suppressed by a richer assemblage of five enemies. Whilst this finding contrasts with that of Wilby et al. (2005), the trend within each species differs and is consistent with complex life cycle pests requiring multiple enemies in order to be maximally exploited by consumers. In our study system, the eggs, larvae and adults of *P. oleae* are found in different micro habitats so, as in the case of the lepidopteran in the laboratory study by Wilby et al. (2005) to be more weakly controlled by a single enemy taxon. In contrast, *E. olivina* adults and nymphs aggregate in the olive flowers where even a single taxon enemy is able to exert a high level of exploitation of the prey resource. This corresponds with the hemipteran prey type in the study by Wilby et al. (2005).

The ant genus *Tapinoma* has previously been reported to have a detrimental effect on other natural enemies in olive groves (Morris et al. 1999b; Pereira et al. 2004). High abundance of *Tapinoma* was associated, in the present study, with low abundance of all other natural enemies, except for *A. nemoralis*. In particular, there was a negative

correlation between *Tapinoma* and *D. punctum*, which is consistent with the operation of intra-guild predation. Indeed, during fieldwork, it was common to see *Tapinoma* descending trees carrying predated *D. punctum* (D. Paredes, personal observation). This effect could disrupt the biological control that *D. punctum* exerts on *E. olivina*. *Euphyllura olivina* was also associated to another natural enemy, *A. nemoralis*, in accordance with the results found by other authors in pear orchards (Scutareanu et al. 1999; Shaltiel and Coll 2004).

This predator overwinters in adult stage (Sigsgaard et al. 2006), particularly in natural vegetation adjacent to the orchard (Horton and Lewis 2000; Chapter 4). Its presence in the orchard is probably mediated by herbivore induced plant volatiles (HIPVs) produced by attacked trees (Drukker et al. 1995). Thus, when *E. olivina* reaches high abundance, HIPVs are likely to induce an increase of *A. nemoralis*. This is a key finding because *A. nemoralis* was also related with low abundance of *P. oleae*. When adults of *A. nemoralis* arrive to the tree, they lay the eggs of the next generation. Due to their small size, the offspring do not have any other available prey but the eggs of *P. oleae*, thus reducing the abundance of this pest. As a result of this process, *A. nemoralis* might be highlighted as one of the most effective biological control agents against *P. oleae*.

Anthocoris nemoralis is possibly the most important predator of *P. oleae* during this generation, but clearly not the only one. An assemblage formed by the spider families Araneidae and Linyphiidae, and the green lacewing *C. carnea* was also associated with low abundances of *P. oleae*. These groups might fulfil complementary functional roles determined by the way they catch prey (Straub et al. 2008; Uetz et al. 1999). Araneidae is an orb weaver spider that makes orbicular webs placed vertically, whereas Linyphiidae, sheet weaver spiders, make tangled web placed horizontally. Both families can potentially predate on the adults of *P. oleae* when they fly within the olive canopy. *C. carnea*, on the other hand, is a branch dweller that predate on the eggs and larvae of *P. oleae*. Overall, the presence of these predators in the orchard can also be a promising option to reduce *P. oleae* populations.

The predator assemblage formed by the predatory Heteroptera *B. ferreri*, *P. coccineus* and *D. punctum*, the ant genera *Camponotus* and *Plagiolepis*, and the spider family Thomisidae, were associated with high abundance of *P. oleae*. In the case of *B. ferreri*

and *P. coccineus*, these species coexist with *A. nemoralis* at nymphal stages, which are susceptible to predation. Thus they are likely to act as alternative prey that disrupt the biological control that *A. nemoralis* exerts on *P. oleae* (Koss and Snyder 2005). In addition, spider species from the Thomisidae family, as well as *Camponotus* and *Plagiolepis*, can prey on *A. nemoralis* as reported in other studies (Fataye and Taffin 1989; Khoo and Chung 1989), and would therefore be involved in an intra-guild predation process which would ultimately dampen the pressure that *A. nemoralis* exerts on *P. oleae* (Finke and Denno 2004).

Overall, large assemblages of natural enemies appear to be associated with weaker pest suppression than are single-best taxa or simple assemblages of up to five spider and insect predators. For a complex lifecycle pest lepidopteran, the single-best predator taxon was associated with weaker pest suppression than was evident for the simple life cycle hemipteran. The statistical approach used in the present study offers scope to explore the relationship between biodiversity and ecosystem function and merits testing in a wider range of agricultural systems. Ultimately, such approaches could be a useful guide to optimising ecosystem services such as biological control by allowing identification of the key aspects of diversity to promote in strategies such as habitat manipulation.

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7

Is ground cover vegetation a good management strategy for pest control?
Insights from a long-term regional assessment in perennial crops

Summary

Ground covers are often used in conservation biological control in perennial crops but studies have yielded inconsistent effects with positive, null or negative effects on pest control. Such divergence might arise from differences at the local scale (e.g. crop management and land use history), the landscape or regional context (e.g. crop diversity, presence of patches of natural or semi-natural vegetation), or the climatic conditions of the area at the time when the study was conducted. In this study, we present the conclusions from a long-term regional monitoring program conducted on four pest species (*Bactrocera oleae*, *Prays oleae*, *Euphyllura olivina*, *Saissetia oleae*) in 2,528 olive groves in Andalusia (Spain) from 2006 to 2012. Generalized linear mixed effect models were used to analyse the effect of ground cover on different response variables related to pest abundance, while accounting for variability at local, landscape and regional scales. The analysis revealed a negligible effect of ground cover on the abundance of olive pests. In contrast, local and landscape scale random factors explained a large proportion of the variability of pest abundance for all response variables. This highlights the importance of local and landscape-related variables in biological control and the potential effects that might emerge from their interaction. We point to perennial vegetation surrounding the field as a potential avenue for biological control research that should receive more attention in the future.

Este capítulo reproduce íntegramente el siguiente artículo:

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7.1 Introduction

Habitat management is a conservation biological pest control strategy focused on manipulating the environment to enhance natural enemy populations (Landis et al. 2000; Paredes et al. 2013). One of the practices most typically adopted in perennial crops is the installation and management of ground cover (Boller et al. 2004), which often consists of an inter-tree herbaceous vegetation strip, although eventually it can extend as a continuous covering on the ground (Smith et al. 1996). Groundcovers can consist of single species or a polyculture mainly of the families Poaceae and Fabaceae (McClure et al. 1982; Stephens et al. 1998), aromatic plants (Song et al. 2010; Beizhou et al. 2011), or simply self-regenerating vegetation (Silva et al. 2010; Aguilar-Fesnellosa et al. 2011). Ground covers can improve the diversity of vegetation, especially if replacing bare ground, and create new habitat structure (Landis et al. 2000). As a result, the abundance (Silva et al. 2010) and diversity of natural enemies increase (Beizhou et al. 2011; Ditner et al. 2013), which might promote higher rates of predation and parasitism of insect pests by natural enemies (Price et al. 1980).

Despite any enhancement of the third trophic level by the use of ground covers, it is still uncertain this translates into reduced pest densities. Much of the existing literature focuses on the effects of ground covers on natural enemies, implicitly assuming that an increase in the abundance or diversity of the natural enemies will lead to a decrease in pest abundance. However, some studies have demonstrated that this does not consistently occur because intraguild predation and other biotic processes might hamper the impact of natural enemies on herbivores (Rosenheim et al. 1995; Hodge 1999; Fink and Denno 2004). Further, those studies that explicitly investigate the effects of ground cover on herbivore abundance give inconsistent evidence (Simon et al. 2010 and

references herein). For example, according to different studies ground cover in peach orchards could either decrease (Dong et al. 2005; Wan et al. 2011) or increase the abundance of pests (McClure et al. 1982; Meagher and Meyer 1990). Their use in other orchards (apple, pear, citrus, olive) has yielded likewise either positive or null results in terms of effective biological control (see **Table 1.1** for a comprehensive compilation of the literature).

What cause such contrasting results? Possible factors include differences in local conditions (e.g. crop management, land use history), the landscape context (e.g. crop diversity, surrounding natural or semi-natural vegetation), and the regional context (e.g. climatic conditions of the region at the time when the study was conducted) (Thies and Tschardtke 1999; Landis et al. 2000; Logan et al. 2006), all of which can potentially modify the response of pests to ground cover.

Factors operating at such different scales, from local to regional, might moderate or mask the effect of ground cover in studies conducted at one single locality and that have no, or little temporal replication. In this study we present evidence from a long-term (2006-2012) regional assessment conducted in 2,528 olive orchards in the Andalusia region of Spain in order to: (1) identify the effect of ground cover on the abundance of pest herbivores and (2) quantify different sources of random variability at local, landscape and regional scales. Through this research, we aim to provide a robust conclusion on the utility of ground covers in olive orchards. Our study is unique in terms of the large spatial (2,528 orchards) and temporal (seven years) replication of samples using the same methodology, which allows detection and quantification of the fixed effect of ground cover on different response variables while accounting for non-specific random variance at the local, landscape and regional scale.

7.2 Material and methods

7.2.1 Data collection

The Warning and Information Plant Protection Network (WIPPN) of Andalusia (Spain) collected data. This network monitors the populations of potentially dangerous arthropods and provides guidelines to farmers on how to treat pests. It has several monitoring stations (MS) spread throughout the region, each covering an area of ca. five hectares. Since 2006, the WIPPN has gathered a large amount of data on olive pest

numbers as well as agronomic factors such as whether ground covers are used (**Figure 3.4**). In this work we focus our attention on four of the most common pests found in this crop: *Prays oleae* (the olive moth), *Bactrocera oleae* (the olive fly), *Euphyllura olivina* (the olive psyllid), and *Saissetia oleae* (the olive scale).

7.2.2 Study species and response variables

For each of the four different pest species we selected response variables that represent -directly or indirectly- population size-related measures and for which there were enough observations (> 250) in the database to conduct reliable statistical analyses (**Table 7.1**).

7.2.2.1 *Prays oleae*

To measure abundance of adults, two funnel traps, baited with the sex pheromone Z-7 tetradecenal, were located in every MS and were checked every week from the beginning of March to the end of November. These traps catch adults from all three generations. The leaf and flower generations partly overlap through time but can be distinguished from the fruit generation. In addition, 400 inflorescences were sampled at each MS and the percentage of inflorescences with larvae was used as a proxy of population size of larvae of the fruit generation. Similarly, a total of 400 olive fruits were taken per MS and the percentage of fruits with larvae of the fruit generation was calculated (**Table 7.1**).

7.2.2.2 *Bactrocera oleae*

Populations of this insect were estimated weekly at each MS from the beginning of June to the end of December by means of three Mc-Phail traps and three sticky traps baited with the pheromones diammonium phosphate and dioxaspiro [5.5] undecane, respectively. The damage caused by this insect was also estimated by counting the number of fruits (out of 400 per MS) that had any sign of damage by olive fly (**Table 7.1**).

7.2.2.3 *Euphyllura olivina*

The number of inflorescences, out of 400 per MS, which had nymphs of olive psyllid was used to estimate the population density of this insect (**Table 7.1**).

7.2.2.4 *Saissetia oleae*

To quantify the presence of this pest, the total number of individuals caught in samples of 200 shoots was counted weekly at each MS (**Table 7.1**).

7.2.3 Data processing and analyses

We used the maximum value attained throughout the year for those response variables that were measured weekly. To account for variability at the landscape scale, we compared paired samples of MSs with ground cover and those with bare soil. We achieved this by geographically searching for the closest MS with bare soil to each MS with ground cover, up to a maximum of 10 km distance. Pairing was done within years and cultivars in order to maintain comparability. This process left out some unpaired MS. In addition, not all the response variables were systematically measured in all MS every year. Consequently, the number of observations used for analysis was not constant for each response variable (**Table 7.1**).

Table 7.1 Response variables used for each of the four species analysed in this study

Species	Response variable	GLM error distribution	Number of monitoring stations used
<i>P. oleae</i>			
	Funnel traps Adults generation 1&2	Poisson	2418
	Larvae / inflorescence	Binomial	1984
	Funnel traps Adults generation 3	Poisson	1114
	Larvae / fruit	Binomial	2160
<i>B. oleae</i>			
	Funnel traps Adults	Poisson	2118
	Sticky traps Adults	Poisson	2528
	Damaged fruits	Gaussian	754
<i>E. olivina</i>	Nymphs / inflorescence	Binomial	276
<i>S. oleae</i>	Living form / shoot	Poisson	354

Family error used in the generalized linear mixed models, and number of observations (i.e. monitoring stations) available for each response variable.

We used generalized linear mixed models (GLMMs) to analyse the effect of ground cover on the different response variables by accounting for random effects at different scales: ‘plot’ (MS site), ‘landscape’ (MS pair), and ‘regional’ (MS year). Depending on the nature of the response variable, we assumed a gaussian, Poisson or binomial distribution of errors (**Table 7.1**). Random factors were used to model potential

structures of autocorrelation in the dataset, specifically: (1) plot represents local scale variability for MS that have been sampled at different years, and might thus have a similar response throughout time due to prevailing management practices, land use history, and/or topographical features; (2) pair refers to the geographical pairing of MS. Paired MS might share a common response to pests, regardless they have ground cover or bare soil, due to landscape-scale factors such as crop diversity or presence of patches of natural or semi-natural vegetation; and (3) year represents particular macro-climatic conditions that might equally affect all plots at the regional level, as it is well known that some years are climatically more suitable for pest outbreaks than others (Martinat 1987; Logan et al. 2006).

We built all possible combinations of random and fixed factors. Overall we fitted 15 models that were compared using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). Models with a difference in AIC > 2 indicate that the worse model has virtually no support and can be omitted from further consideration. Following Nakagawa and Schielzeth (2013) we calculated the R^2 to have an account of the variability supported by the model. These authors also include two measurements of this parameter: (1) a marginal R^2 (R_m^2) that only takes into account the variability explained by fixed effects; and (2) a conditional R^2 (R_c^2) that accounts for the variability supported by both the fixed and random effects. When ground cover was included in at least one of the best models we quantified its effect in relation to the different sources of random variability (local, landscape and regional) for each response variable. To achieve this, we calculated the difference between ground cover and bare soil from the fixed effects estimated model parameters, and added a random error from the corresponding variance term estimated by the model at each scale of variability. We repeated this procedure 1000 times and plot the 95% confidence intervals of such predictions. To perform the analyses we used the package 'lme4' (Bates et al. 2013) written for the R environment (R Development Core Team 2012).

7.3 Results

Model selection indicated that there were either one or two best models for each response variable. In all cases, except for *E. olivina* and *S. oleae*, at least one of the best models included the fixed and all the random effects (**Table 7.2**).

Alternative best models for some response variables (*P. oleae* funnel traps in all generations; *B. oleae* funnel traps and fruit damage; *S. oleae*) excluded the fixed effect. Finally, for *E. olivina* and *S. oleae*, the best model excluded the regional-scale random effect (**Table 7.2**). For all best models, we found a much higher conditional R^2 (R_c^2) than the marginal R^2 (R_m^2) (**Table 7.2**).

Model estimations showed that, even if ground cover was selected in the best model, it had a negligible effect in absolute terms as compared to random variability. This was particularly the case for local (i.e. plot) and landscape (i.e. pair) scales, although regional variability was also important for most of the response variables (**Figure 7.1**).

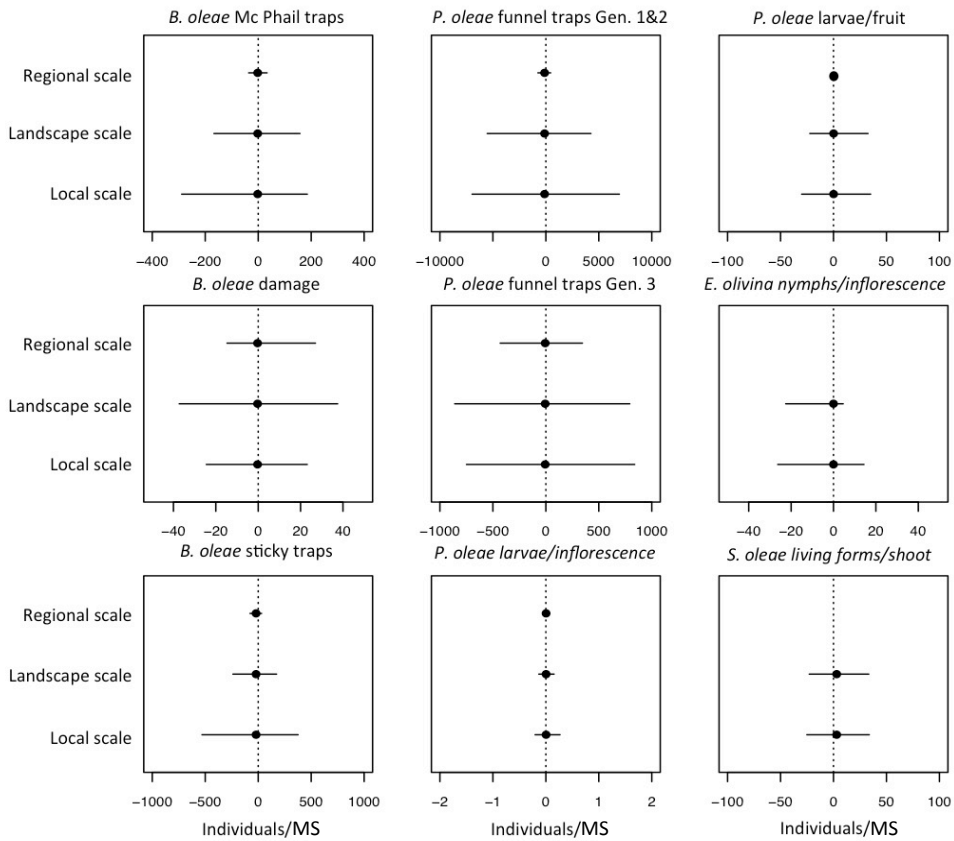


Figure 7.1 Model estimations for the differences between ground cover and bare soil for all the response variables. Bars represent a 95% of the confidence interval of the random effects predictions ($\pm\sigma^2$) at a local, landscape and regional scale. Positive values represent an increase of response variable whereas negative values represent a decrease of the response variable.

Table 7.2 Comparison of alternative models (using AIC) for the response variables tested in the study. The best model (lowest AIC) is indicated in boldface type. The marginal (m) and conditional (c) R^2 refer to the best model.

Model	Species and response variable										
	<i>P. oleae</i>			<i>B. oleae</i>			<i>E. olivina</i>		<i>S. oleae</i>		
Fixed effect	Funnel traps generation 1&2	Funnel traps generation 3	Larvae/ inflorescence	Larvae/ fruit	Funnel traps	Sticky traps	Damaged fruits	Presence/ inflorescence	Presence/ shoot		
Ground cover											
Random effect											
No	7148856.00	651674.10	59937.78	212352.6	286552.5	409016.50	5151.03	8841.59	1107140.00		
Local	1472573.00	69880.42	18800.90	86147.74	87783.54	113752.80	5131.30	2491.27	116458.10		
Landscape	1153317.00	104143.30	16803.58	69063.21	73057.67	100578.20	5064.25	2015.06	305188.30		
Regional	6107724.00	492291.50	45024.71	187061.4	242004.7	347386.70	5049.47	7223.38	1025274.00		
Local+Landscape	111208.90	14187.12	7935.64	23439.52	17209.24	26004.65	5045.40	1294.32	12803.75		
Local+Regional	1020315.00	55629.47	16280.28	77530.91	69858.43	89974.97	5023.11	1673.95	76446.79		
Landscape+Regional	1153103.00	103.970.90	16661.74	68987.29	72832.11	100404.50	4995.03	2009.70	305190.30		
Local+Landscape+Regional	111053.00	14019.72	7803.70	23397.89	16982.35	25813.69	4978.63	1297.49	12805.75		
Local	1472948.00	70113.51	18799.81	86150.07	88040.37	113771.00	5130.32	2502.77	116456.30		
Landscape	1154130.00	107205.3	16841.12	69461.36	73463.42	100681.90	5063.33	2026.55	318915.90		
Regional	6108537.00	495353.6	45059.58	187405.7	242410.4	347490.30	5048.25	7233.54	1038998.00		
Local+Landscape	111212.40	141858.92	7940.64	23466.91	17207.87	26012.30	5044.49	1300.44	12802.48		
Local+Regional	1033389.00	55739.87	16298.67	77539.27	70436.83	89991.66	5021.93	1683.19	76445.08		
Landscape+Regional	1153916.00	107033	16699.28	69385.44	73237.86	100508.10	4994.11	2021.19	318917.90		
Local+Landscape+Regional	111055.70	14018.45	7810.15	23424.78	16981.39	25821.62	4977.29	1303.72	12804.48		
R_m^2	0.00080	0.00043	0.00165	0.00562	0.00050	0.00459	0.00046	0.01245	0.00528		
R_c^2	0.82426	0.88419	0.41615	0.56952	0.69629	0.80045	0.62922	0.73679	0.83203		

The best model (lowest AIC) is indicated in boldface type. The marginal (m) and conditional (c) R^2 refer to the best model.

7.4 Discussion

The results of this study indicated that ground covers, as a single entity and compared to bare ground, are not an effective measure to reduce pest abundance in olive groves. This is evident in the absence of this term in some of the best fit models, the low amount of variability explained by this factor in those models where it was present, and its small absolute effect - as quantified by estimated model parameters - in relation to the random factors. In contrast, random effects, particularly at local and landscape scales, explained a great proportion of the observed variability in all the response variables. Such factors represent the effect of variables operating at different spatial and temporal scales, whose variability has not been specifically measured, and which might have an influence in the response variable. Although the processes operating behind random factors are unknown, here we provide an account of potential variables that might be causing the high variability observed in pest abundance or related response variables (e.g. damage to crop) at different spatial scales.

At the local scale, crop management related issues such as intensity of pesticide application, land use history, topography or micro-climatic features, might have an important effect on pest abundance. The composition of ground cover (Begum et al. 2006), its density (Collof et al. 2013), the width of the strip (Hardman et al. 2011), or the height of grasses might also have an influence on pest abundance (Tsitsilas et al. 2011). Humidity can affect herbivores such as *S. oleae*, as larger populations of this insect have been found near rivers or creeks (De Andrés 1991). The abundance of *B. oleae*, has been demonstrated to be influenced by site elevation (Castrignano et al. 2012). Another factor that could influence pest populations is the history of pesticide use (Croft and Brown 1975). An overuse of these substances in the recent past could depress the local community of natural enemies thereby favouring herbivores. Further, a lack of surrounding non-crop vegetation would increase the detrimental effects of pesticide, as natural enemies will have no refuge from which to recolonize sprayed crops (Landis et al. 2000; Bianchi et al. 2006; Simon et al. 2010).

Landscape-scale factors relate largely to the composition and connectivity of vegetation including other crops, natural or semi-natural vegetation, at ranges up to 10 km from the crop that are known to be able to affect the movement of natural enemies into the crop (Thies and Tschardtke 1999; Bianchi et al. 2006; Perovic 2010). In Andalusia, as well

as in other Mediterranean regions, olive groves range from the highly productive with low landscape diversity; other groves, typically in mountainous areas, where productivity is lower and landscape heterogeneity high; and intermediate sites set in a mosaic of differing land uses (Duarte et al. 2009). These differences in landscape context can certainly have an influence on pest abundance (Thies and Tschardt 1999; Bianchi et al. 2006; Rusch et al. 2013). In olive groves, areas of herbaceous vegetation and areas of woody vegetation near olive crops, and smaller patches of woody vegetation within olive groves, decreased the abundance of *P. oleae* and *E. olivina* (Chapter 5). Landscape features such as mean patch size, edge density and Shannon landscape diversity index, might likewise help reduce *B. oleae* abundance (Bocaccio and Pettachi 2009; Ortega and Pascual 2013). This does not necessarily mean that the more the natural vegetation the most effective the biological control. Indeed, some studies seem to point out to complex interactions between different landscape features and ground cover (Chapter 4), sometimes reinforcing their mutual role in biological control, and some other times counteracting their effects (Martin et al. 2013). For example, in chapter 4 was detected that when both habitats were present in the crop, the abundance of some groups of natural enemies (spider and parasitoids) was positively influenced by adjacent vegetation, whereas this effect was lower or even reversed in bare soil plots. Habitats provided by surrounding natural vegetation can also produce the opposite effect by removing, rather than providing, natural enemies to the crop (Blitzer et al. 2012).

Finally, at regional scales, we suggest inter-annual climatic variability as the factor that can have a major influence on pest abundance. Changes in temperature and humidity could alter the phenology of pests and natural enemies and, therefore, influence insect population growth rate (Martinat 1987; Logan et al. 2006). In chapter 5, we already detected a high variability between two consecutive years in the response of *E. olivina* and *P. oleae* to ground cover and different surrounding natural vegetation features, and attributed these changes to climatic variability between years. Similar behaviour has been described for *P. oleae* by De Andrés (1991).

From a farmer perspective, local conditions are too varied to be accounted for when outlining pest control strategies. Similarly, nothing can be done to account for inter-annual climatic variability, even though the response of pests to any treatment,

including ground cover, might be dependent on climatic conditions (Hardman et al. 2013). Landscape-scale factors, on the other hand, can be -at least partly- controlled by farmers and are thus subjected to be included in the corollary of good farming practices. Thus, future research should pay more attention to the landscape context, particularly to perennial non-crop vegetation surrounding or nearby the crop, and to the interactions between these structures and ground cover. Finally, although our study has demonstrated that ground cover by itself is not particularly efficient in terms of biological control, we acknowledge that other reasons, such as soil fertility and prevention of soil erosion (Cullen et al. 2008; Hartwig and Ammon 2002), or pollination enhancement (Tscheulin et al. 2011), might justify its use in orchards.

7.5 References

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8

Discusión

Evaluar la capacidad de las infraestructuras ecológicas para el control biológico por conservación de plagas de olivar no es una tarea fácil, ya que se han detectado multitud de procesos, tanto directos como indirectos, que pueden condicionar el efecto de estas estructuras en las poblaciones de distintos grupos de artrópodos. No obstante, la presente tesis doctoral intenta dar un paso más hacia la adquisición de conocimientos en este campo de la ciencia y más concretamente en el cultivo del olivo, donde la implantación de estas técnicas tiene gran potencial pero han sido poco estudiadas. Este trabajo presenta un enfoque innovador por varios aspectos. En primer lugar, y hasta dónde alcanza nuestro conocimiento, éste es uno de los primeros trabajos en los que se han analizado los efectos conjuntos de diferentes infraestructuras ecológicas sobre la abundancia de artrópodos. En segundo lugar, la detección de controversias (un aumento de la abundancia de enemigos naturales en zonas con cubierta vegetal no redundó en una disminución de la abundancia de las plagas en las mismas zonas) ha propiciado el estudio de las relaciones de los enemigos naturales entre sí y de estos con las plagas. Por último, se ha utilizado una amplia escala temporal (seis años de observaciones) y espacial (más de 2.528 olivares repartidos por toda la Comunidad Autónoma de Andalucía) para analizar el efecto de la cubierta vegetal sobre distintas especies de plaga, lo cual ha aportado una visión global del papel de esta estructura en el control biológico.

En el capítulo 4 se detectaron efectos sinérgicos entre la cubierta vegetal y las manchas de vegetación naturales en algunos grupos de enemigos naturales. Arañas y parasitoides fueron más abundantes en parcelas con cubierta vegetal mientras que esta estructura no afectó a los heterópteros depredadores. Grandes manchas de vegetación leñosa y herbácea influyeron más en la abundancia de enemigos naturales que las manchas

pequeñas. El efecto de la vegetación natural adyacente fue diferente para cada grupo y dependió de la presencia de cubierta vegetal. Cuando ambas estructuras estaban presente en el cultivo, parasitoides y arañas fueron positivamente influenciados por la vegetación adyacente, mientras que este efecto fue menor o incluso opuesto en zonas de suelo desnudo, sobre todo en el caso de las manchas de vegetación herbácea para arañas.

Distintos estudios han mostrado la preferencia de las arañas por los hábitats herbáceos (Pluess et al. 2010). Cuando estos hábitats se encuentran dentro del cultivo, como es el caso de las cubiertas vegetales, las arañas pueden utilizar los árboles, debido a su proximidad, como fuente alternativa para encontrar alimento y refugio, particularmente después de la senescencia del sustrato herbáceo (Landis et al. 2000; Bianchi et al. 2006). Sin embargo, la vegetación herbácea localizada alrededor del cultivo, puede ser igualmente atractiva para las arañas, pero reducirá la abundancia de las mismas en la copa de los árboles ya que potencialmente favorecen la migración fuera del cultivo (Schmidt y Tschardt 2005). En cuanto a los parasitoides, su dependencia de los hábitats herbáceos, dentro y alrededor del cultivo, así como de la vegetación leñosa, es muy alta. De hecho, en ausencia de estas estructuras (ej. suelo desnudo y ausencia de vegetación adyacente) los modelos predicen una abundancia próxima a cero, lo cual podría ser debido a que los parasitoides son enemigos naturales especialistas, por lo que su respuesta a la complejidad del paisaje a pequeña escala es mucho mayor (Boccaccio y Petacchi 2009; Chaplin-Kramer et al. 2011). Por el contrario, los heterópteros depredadores parecen no estar afectados por este tipo de hábitats. La vegetación herbácea y las pequeñas manchas de vegetación leñosa localizadas cerca y dentro del olivar no ejercen un efecto importante sobre su abundancia. Tres de las cuatro especies (*P. coccineus*, *B. ferreri* y *D. punctum*) son míridos encontrados en estado de ninfa al comienzo de la estación, lo que implica que se han desarrollado en el árbol sin ninguna interacción con la cubierta vegetal. La única especie encontrada en estado adulto fue *Anthocoris nemoralis*, la cual puede invernar en los hábitats naturales de la zona (Horton y Lewis 2000), lo que podría explicar el efecto positivo que sobre la abundancia de esta especie ejercen las grandes manchas de vegetación leñosas.

En vista de los efectos que la cubierta vegetal causa en arañas y parasitoides, cabría esperar que en zonas en las que esta estructura estuviera presente las poblaciones de

plagas fuesen menores que en aquellas zonas donde el suelo estuviera desnudo. No obstante, en este estudio (Capítulo 5), al igual que en trabajos previos (Aldebis et al. 2004; Rodríguez et al. 2009), la cubierta vegetal tuvo un efecto nulo en la abundancia de *P. oleae* y *E. olivina*. Este hecho podría reflejar una falta de sincronismo entre estas especies de herbívoros y los enemigos naturales que han mostrado una respuesta a la presencia de las cubiertas vegetales sobre todo arañas, las cuales alcanzan su población máxima a mediados de agosto, no coincidiendo con las plagas (Perdikis et al. 2011). Alternativamente, también podría ocurrir que los enemigos naturales favorecidos por las cubiertas vegetales no utilizasen ni a *P. oleae* ni a *E. olivina* como presas, como podría ser el caso de los parasitoides, ya que la mayor parte de las familias que han incrementado sus poblaciones no son específicas de las plagas.

Las manchas de vegetación natural sí que tuvieron, por el contrario, un efecto positivo en el control biológico de plagas. En concreto, la presencia de grandes manchas de vegetación leñosa redujo la abundancia de *P. oleae* y la de pequeñas manchas de vegetación leñosa disminuyó la abundancia de *E. olivina*. Estos resultados son los más consistentes de los obtenidos ya que no cambian entre los dos años. Los demás presentaron variabilidad entre años en el cambio proporcional de la abundancia de las dos especies plaga lo cual podría indicar que las condiciones climáticas juegan un papel importante en modular la respuesta de las plagas a su ambiente (Martinat 1987; Logan et al. 2006). Las reducciones en la abundancia de las plagas podrían estar asociadas al incremento observado de las poblaciones de heterópteros depredadores, ya que estas plagas son altamente específicas del olivar.

Para corroborar las tendencias observadas y determinar la fuente de controversia se decidió explorar las relaciones entre distintos grupos de enemigos naturales y las plagas *P. oleae* y *E. olivina*. Uno de los resultados más relevantes del capítulo 6 puso de manifiesto que elevadas poblaciones de la hormiga *Tapinoma* estaban asociadas con bajas abundancias de todos los otros enemigos naturales, excepto en el caso del depredador heteróptero *A. nemoralis*. En particular, se detectó una correlación negativa entre *Tapinoma* y el mío *D. punctum*, la cual podría indicar un proceso de depredación intragremial. Distintos estudios han puesto de manifiesto que las hormigas del género *Tapinoma* tienen un efecto perjudicial sobre otros enemigos naturales en el olivar (Morris et al. 1999; Pereira et al. 2004). De hecho, es frecuente observar en

campo como las hormigas de este género descienden de los olivos llevando *D. punctum*, lo cual podría alterar el control biológico que *D. punctum* ejerce sobre *E. olivina* (D. Paredes, observación personal).

E. olivina también estuvo asociada a otro enemigo natural, *A. nemoralis*, al igual que ocurre en otros cultivos como el peral (Agustí et al. 2003; Shaltiel y Coll 2004). Este depredador inverna en estado adulto en la vegetación adyacente a los cultivos, como se observó en el capítulo 4 (Horton y Lewis 2000). Su presencia en el cultivo está, probablemente, mediada por los volátiles que las plantas emiten inducidos por la presencia de los herbívoros (Drukker 1995). Así, se puede pensar que cuando *E. olivina* alcanza una elevada abundancia en el árbol, éste emite una serie de volátiles que inducirían un incremento de las poblaciones de *A. nemoralis*. Este hecho es de gran importancia dado que como resultado de los análisis realizados, *A. nemoralis* fue asociado con una baja abundancia de *P. oleae*. Cuando los adultos de *A. nemoralis* llegan al árbol, dejan los huevos de la próxima generación, y debido a su pequeño tamaño, los neonatos no tienen más presa disponible que los huevos de *P. oleae*, por lo que es de suponer que inciden sobre los mismos reduciendo su abundancia. Como resultado de este proceso, se confirmaría que *A. nemoralis* es uno de los agentes más efectivos de control biológico de la generación antófaga de *P. oleae* (Morris et al. 1999).

Además de *A. nemoralis*, se ha identificado en el olivar un conjunto de depredadores formado por dos familias de arañas, Araneidae y Linyphiidae, y el neuróptero *C. carnea* que también se asociaban con bajas abundancias de *P. oleae*. Estos grupos podrían cumplir funciones complementarias determinadas por la forma en la que capturan a sus presas (Straub et al. 2008). Por el contrario, el conjunto formado por los heterópteros depredadores *B. ferreri*, *P. coccineus* y *D. punctum*, las hormigas del género *Camponotus* y *Plagiolepis*, y las arañas de la familia Thomisidae, se asociaron a elevadas poblaciones de *P. oleae*. Las especies de arañas de la familia Thomisidae, así como las hormigas de los géneros *Camponotus* y *Plagiolepis*, pueden depredar sobre *A. nemoralis* como se ha observado en otros estudios (Khoo y Chung 1989), pudiéndose producir un proceso de depredación intragremial y, en última instancia, una reducción de la presión que *A. nemoralis* ejerce sobre *P. oleae*.

Al parecer, la abundancia de plagas está más sujeta a la presencia de manchas de vegetación natural y de los enemigos naturales que éstas albergan, que a la presencia de una cubierta vegetal. No obstante, a lo largo del trabajo se han detectado determinadas circunstancias (paisajísticas y climáticas) que podrían determinar el papel de la cubierta vegetal en el control biológico de plagas. Éstas podrían estar enmascarando el verdadero efecto de esta estructura, emitiendo conclusiones poco válidas si los estudios no tienen en cuenta estas características o son desarrollados a una escala local. El análisis sobre el efecto de la cubierta vegetal en una amplia zona de estudio y a una gran escala temporal aportó evidencias mucho más rotundas acerca de la utilidad de la cubierta vegetal en el control biológico por conservación de plagas del olivo.

Los resultados del capítulo 7 indicaron que la cubierta vegetal, como una sola entidad y comparada con suelo desnudo, no es una medida efectiva para reducir la abundancia de plagas en olivares. La variabilidad explicada por factores aleatorios relacionados con las condiciones propias de la parcela (escala local), del contexto paisajístico (escala de paisaje) y de los cambios climáticos entre años (escala regional) fue mucho mayor que la debida a la cubierta vegetal.

A escala local, las características físicas de la parcela (orografía, características microclimáticas), así como las propias asociadas al manejo de la finca (intensidad de los pesticidas aplicados, historia de uso de la tierra), podrían tener un importante efecto en la abundancia de las plagas. La composición de la cubierta vegetal (Begum et al. 2006), su densidad (Collof et al. 2013), la anchura de la franja (Hardman et al. 2011), o la altura de las hierbas que la componen también podrían tener un efecto en la abundancia de plagas (Tsitsilas et al. 2011). Otro factor que puede influenciar las poblaciones de plagas es la historia de uso de pesticidas (Croft y Brown 1975). Un abuso de estas sustancias en el pasado reciente pudo reducir las poblaciones de enemigos naturales a niveles poco útiles para el control biológico. Además, la falta de manchas vegetación natural incrementaría el efecto perjudicial de los pesticidas, debido a que los enemigos naturales no tendrían lugares en los que refugiarse y desde donde recolonizar los cultivos tratados (Landis et al. 2000; Bianchi et al. 2006; Simon et al. 2010).

Factores a escala de paisaje se refieren, en gran parte, a la composición y la

conectividad de la vegetación, a distancias de hasta 10 km del campo de cultivo. Estas estructuras son capaces de influir en el movimiento de los enemigos naturales en el cultivo (Thies y Tschardtke 1999; Bianchi et al. 2006; Perovic et al. 2010). En Andalucía, al igual que en otros países mediterráneos, existen muchas tipologías de olivares que van desde los altamente productivos con poca diversidad de paisaje; pasando por los de áreas montañosas, que tienen una productividad menor pero alta diversidad paisajística; y acabando por olivares que se encuentran inmersos en zonas con diversos cultivos alrededor (Duarte et al. 2009). Estas diferencias en el contexto paisajístico pueden tener gran influencia en la abundancia de plagas (Thies and Tschardtke 1999; Bianchi et al. 2006; Rusch et al. 2013). Características del paisaje como el tamaño medio de las manchas de vegetación natural, la densidad de borde y la diversidad paisajística pueden ayudar a reducir la abundancia de plagas como *B. oleae* (Bocaccio y Pettachi 2009; Ortega y Pascual 2013). Esto no necesariamente significa que a mayor densidad de vegetación natural mayor control biológico ya que algunas veces puede darse el efecto contrario debido a interacciones negativas entre los organismos pertenecientes al agroecosistema (Martin et al. 2013) o a que estos hábitats producen el efecto contrario retirando, en lugar de proporcionando, enemigos naturales al campo de cultivo (Blitzer et al. 2012).

Por último, a escala regional, se sugiere la variabilidad climática interanual como un factor que puede tener una gran influencia sobre la abundancia de plagas. Como se observó en el capítulo 5, los cambios en la temperatura y la humedad pueden alterar la fenología de las plagas y sus enemigos naturales y, por tanto, influir en la tasa de crecimiento de la población de insectos (Martinat 1987; Logan et al. 2006).

Emitir unas directrices claras acerca del manejo de las infraestructuras ecológicas para el control biológico por conservación de plagas de olivares partiendo de los resultados obtenidos en esta tesis doctoral se torna complicado, más teniendo en cuenta que es razonable pensar que cada tipo de olivar deberá plantear su modo particular de relación con la biodiversidad de forma que sea posible compatibilizar su conservación con el resultado económico (Duarte et al. 2009). No obstante, se puede apuntar a las manchas de vegetación natural, sobre todo leñosas, como aquellas infraestructuras ecológicas cuya presencia mejora el control biológico de plagas del olivo. Más concretamente, este tipo de manchas pueden albergar poblaciones de *Anthocoris nemoralis*, un agente de

control biológico potencial de la generación antófaga de *P. oleae*. Profundizar en las razones de su presencia en el campo, la forma de reforzar sus poblaciones y sus relaciones con otros agentes del agroecosistema es un paso clave si se quiere controlar esta plaga.

Aunque no se ha observado un efecto claro de la cubierta vegetal en el control biológico de cuatro importantes plagas del olivar, ésta contribuye a aumentar la heterogeneidad de hábitat a nivel local, mostrando su utilidad para mantener poblaciones de artrópodos beneficiosos en el campo de cultivo. Un estudio más detallado de su composición, disposición y manejo con el objetivo de optimizar su papel en el control biológico por conservación sería aconsejable ya que permitiría obtener conclusiones capaces de generar directrices de manejo útiles para los agricultores. De todas formas, la cubierta vegetal es recomendada para mejorar otros servicios ecosistémicos como son el reciclado de nutrientes, la prevención de la erosión o el aumento de la polinización (Cullen et al. 2008; Hartwig y Ammon 2002; Tscheulin et al. 2011).

8.1 Bibliografía

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9

Conclusiones

Conclusions

Las conclusiones que se derivan de la presente tesis doctoral son las siguientes:

1a La presencia de cubierta vegetal espontánea incrementa la abundancia de arañas y parasitoides, pero no tiene efecto sobre heterópteros depredadores.

1b Ground cover increases the abundance of spiders and parasitoids but has null effect on predatory Heteroptera.

2a La presencia de grandes manchas de vegetación leñosa puede ayudar a incrementar las poblaciones de arañas y parasitoides, creando hábitats alternativos que podrían propiciar la migración de estos individuos hacia el cultivo. Sin embargo, en ausencia de cubierta vegetal, tales hábitats podrían ser más atractivos para las arañas, probablemente debido a la escasez de recursos existentes en el cultivo.

2b Large woody vegetation patches can help increase the abundance of spiders and parasitoids by providing alternative habitats that may favor the migration of individuals to the crop. However, in the absence of ground cover, such habitats may be more attractive to spiders, probably due to the scarcity of available resources within the crop.

3a La presencia de cubierta vegetal incrementa el efecto positivo que las manchas de vegetación herbácea tienen sobre la abundancia de los parasitoides y reduce el efecto negativo que esta vegetación tiene sobre las arañas.

3b The presence of ground cover increases the positive effect that patches of herbaceous vegetation have on the abundance of parasitoids and reduce the negative effect that this vegetation has on spiders.

4a La presencia de grandes manchas de vegetación leñosa cerca del olivar y de pequeñas manchas de vegetación leñosa dentro del olivar, disminuye consistentemente la abundancia de *P. oleae* y *E. olivina* respectivamente.

4b The presence of large woody vegetation patches surrounding the olive grove and small woody vegetation patches inside the crop, consistently reduce the abundance of *P. oleae* and *E. olivina* respectively.

5a La presencia de cubierta vegetal espontánea, aunque incrementa la abundancia de algunos enemigos naturales, no tiene un efecto sobre la abundancia de *P. oleae* y *E. olivina*.

5b Although ground cover increases the abundance of some groups of natural enemies, it has no effect on the abundance of *P. oleae* and *E. olivina*.

6a Cambios en los factores climáticos entre años afectan a la abundancia de plagas y de enemigos naturales.

6b Changes in climatic factors between years have an effect on the abundance of pests and natural enemies.

7a Una sola especie, como *Anthocoris nemoralis*, o un conjunto relativamente simple de depredadores, tales como los formados por dos familias de arañas (Araneidae y Liniphiidae) y el neuróptero *Chrysoperla carnea*, ejercen un mejor control biológico de las plagas que conjuntos más complejos.

7b Single species such as *Anthocoris nemoralis*, or relatively simple predator assemblages, such as that formed by the spider families Araneidae and Liniphiidae, and the green lacewing *Chrysoperla carnea*, were associated with better biological control than complex assemblages.

8a Factores a escala local, paisajística o regional tiene un papel más importante en el control biológico de plagas de olivar que la presencia o ausencia de cubierta vegetal espontánea.

8b Factors at local, landscape or regional scale have a more important role in the biological control of olive pests than the use or non-use of ground cover.